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WIGO
Model description

**Institutionen för markvetenskap**
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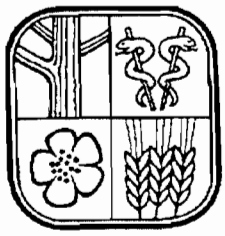
**Rapport 163**
**Report**

**Uppsala 1991**
**ISSN 0348-1816**
**ISRN SLU-HY-R--163--SE**



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# 1 INTRODUCTION

This paper aims to describe the theory of the WIGO (WIllow GrOwth) model. The model considers all biomass and nitrogen flows in a short rotation forest which are of major importance for growth. The description is a tool when using the model and then should be used together with a manual (Eckersten, 1991a). The link to the manual is through the symbols given in the List of symbols. The text always refers to the model and not directly to reality, unless otherwise stated. As regards the validity of the model the reader is referred to the section on Validation and other publications given in the List of references, in which tests of different parts of the model have been made. The software of the model is available from the author on request.

An earlier version of the model was first published by Eckersten *et al.* (1983). Since then the model has been developed considerably and the basic concept of the version presented here was presented by Eckersten & Slapokas (1990) for current year-old shoots. For shoots older than one year the biomass submodel (of the main model) has in some parts been described by Eckersten *et al.* (1989). The reader is referred to these earlier presentations as regards the origin of the equations.

The time step of the model is one day and simulations can be made over several years and include different types of management (harvest, fertilization, defoliation, etc.). It has been developed for willow stands but can be applied on stands of other species as well.

Since the model aims to be a research tool, although also suitable for many practical purposes, it includes possibilities to choose among different hypotheses (see the section on special functions) and will be modified as research makes progress. This model description hence includes some processes not originating from other publications. New or modified equations including these processes are denoted with an asterisk (*). Most changes are only modifications of previously used equations due to the introduction of a pool for easily available assimilates in the plant.

A section of the model description usually starts with a short general summary of its contents (written in italics) followed by a more detailed verbal (and graphic) description of the calculation procedure. The section ends with the mathematical expressions. This enables the model to be understood regardless of whether the reader is familiar with mathematical expressions or not. Also, for the reader who is familiar with equations, this gives a good over-view of the model. The numbers allotted to equations, figures and tables are related to the section number concerned.

# 2 MODEL

The plant and soil consist of several compartments. For the current year growth the plant is divided into the leaf, stem and root compartments and the pool for easily available assimilates and nitrogen, whereas tissues older than one year are treated separately and divided into stem and root. The litter, regardless of the tissue from which it originates, falls into the litter cohort which does not decompose during the current year. The older litter, however, decomposes and is separated into different cohorts in such a way that each year class has its own cohort. Once a year the oldest cohort is transferred to the humus cohort which decomposes slowly. In the soil there is a pool of nitrogen easily available for uptake ($N_{as}$). Each compartment is divided into a biomass (or carbon) part and a nitrogen part, except for $N_{as}$. Conceptually, the model is divided into a biomass submodel and a nitrogen submodel that interact daily (Fig. 200).

The factors linking the two submodels are the nitrogen need for growth of the stand each day and the available nitrogen in the soil after fertilization and mineralization/immobilization, together with the return of nitrogen through the litter produced. This means that, (i) the production submodel has the leaf nitrogen content as an input variable taken from the nitrogen turnover submodel and (ii) the nitrogen turnover submodel, in turn, has the daily growth of leaves, stems and roots and amount of litter as input variables taken from the production submodel (see Fig. 200). The combined model is valid for horizontally uniform stands and the growth is assumed not to be limited by shortage of nutrients other than nitrogen. The time step of the model is one day, and for each day the calculations of the biomass production submodel are made before those of the nitrogen turnover submodel.

Input variables are daily duration of sunshine as a fraction of the maximum possible (can be represented by other radiation variables as well), daily means of air and soil temperatures, the daily application of fertilizer-nitrogen and the soil and plant water factors. The water factors can be simulated with the soil water and heat model called SOIL (Jansson & Halldin, 1980, Jansson, 1991). The leaf thickness (or more precisely the aerial leaf weight) can also be regarded as being a driving variable. However, usually it is considered to be constant and taken as a parameter.

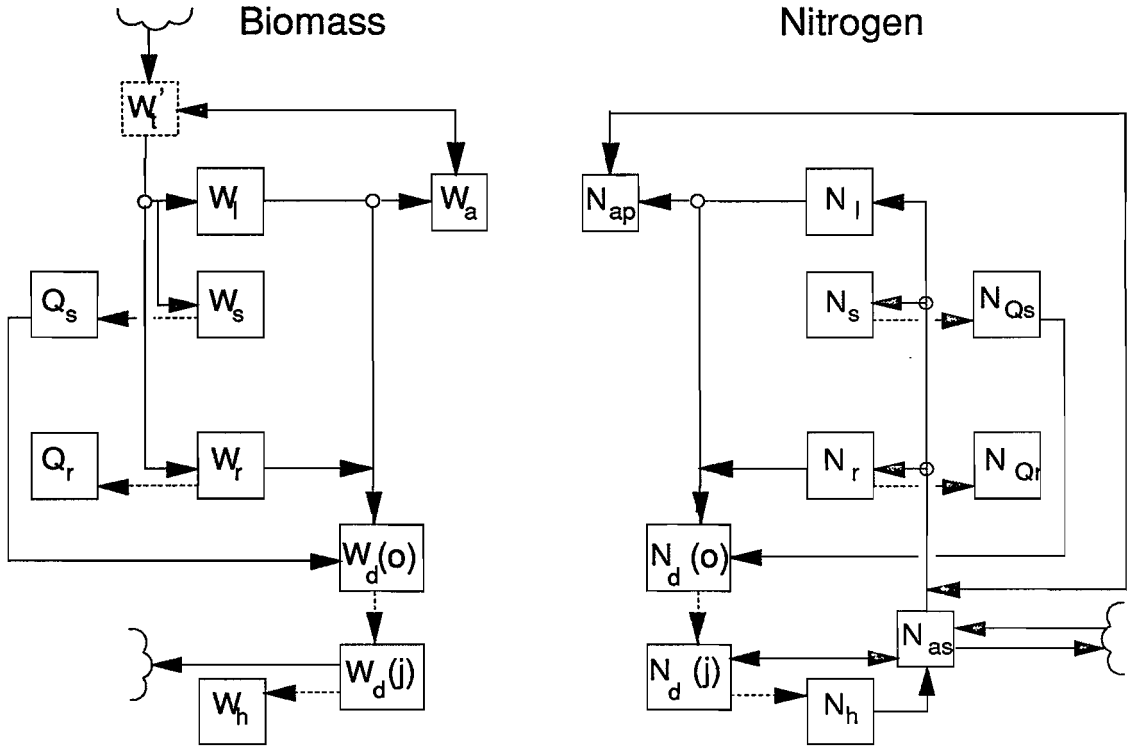



**Figure 200.** Schematic description of the WIGO model consisting of two "submodels": the production submodel and the nitrogen turnover submodel. W and N are biomass and nitrogen respectively. Indices are as follows: a=available pool; ap= available pool in plant; as= available pool in soil; d=litter; h=humus; l=leaf; r=root; s=stem; and t=total. j is the age. $Q_s$ and $Q_r$ are the stem and root biomass older than one year and $N_{Qs}$ and $N_{Qr}$ are the nitrogen contents of these tissues. The prime sign denotes a daily change. Solid lines are daily mass flows whereas dotted lines are annual flows. All major flows of the model are represented in the graph. Those lacking are leaching of N from falling leaves and harvest.

*Schematisk beskrivning av WIGO-modellen. Modellen består av två delmodeller: produktionsmodellen (W) och kväveomsättningsmodellen (N). Q och $N_Q$ är biomassa och kväveinnehållet för vävnader äldre än ett år. Primtecknet betyder ett dagligt flöde. Heldragna linjer är dagliga massflöden och streckade linjer är årliga flöden.*

# 3 BIOMASS PRODUCTION SUBMODEL

## 3.1 Growth

*The daily growth is mainly determined by the photosynthesis rate which increases with light absorption, air temperature, plant nitrogen and water status and leaf thickness. The photosynthesis for a semi cloudy day is achieved by first calculating hourly the photosynthesis of a typical clear and overcast sky, respectively. Daily sums for these conditions represent the maximum and minimum photosynthesis and, by interpolating between them in accordance with the actual radiation, the actual daily photosynthesis is achieved. The total daily growth that is available for structural growth is, in the case of flushing, further increased by easily available assimilates already located in the plant. It is decreased by the amount of assimilates used for respiration.*

The day for start of growth ($t_o$) is determined by the accumulated sum of daily mean air temperatures above $T_1$ °C (which is the lower temperature limit for growth, see below) since a certain day during late winter ($t_T$). Growth starts when this sum exceeds a special day-degree sum ($T_{Sum}$) (Eq. 310). An initial amount of shoot (leaf plus stem) biomass is developed from assimilates stored in the standing biomass and available for flushing ($W_a$). At the start of growth this pool is consumed at a rate proportional to a temperature function ($T_f$) and limited by a maximum daily release ($\delta W_{aMax}$) (Eq. 335).

The assimilates from $W_a$ are partitioned between leaf and stem growth following the ordinary equations for allocation of the daily growth (Eqs. 320-336). At this time the newly formed tissues are supplied with nitrogen from the easily available pools located in the plant ($N_{ap}$) and the soil ($N_{as}$) (see further the section on nitrogen turnover submodel).

Once this flushing has occurred the photosynthesis of the leaves starts and thereby the growth of the plant. The daily total growth per unit of soil surface ($W_t$') is then equal to the canopy gross carbohydrate fixation ($P_d$) reduced by the costs for growth ($r_g$) and maintenance ($r_m$) respiration but plus the release of assimilates stored in the plant ($W_a$'(out)). All these processes are dependent on the temperature response function ($T_f$) which increases linearly from zero for daily mean air temperature (T) below or equal to $T_1$ °C, to unity for T equal to or higher than $T_2$ °C. Above a daily air temperature of $T_3$ °C it decreases at the same rate as it increases for low temperatures (Eqs. 311-312).

$P_d$ is estimated by interpolation, according to the duration of sunshine, between the potential carbohydrate fixation for clear sky conditions ($P_{dc}$) and that for overcast conditions ($P_{do}$). The function for interpolation (M) is a second order polynomial of the daily fraction of sunshine (D) which can be estimated from the daily global radiation (Eqs. 313-314).

$P_{dc}$ for the whole canopy is estimated hourly by integrating the photosynthesis for single leaves ($P=P_mI/(I+I_p)$) over the leaf area index of the whole canopy ($A_{li}$) assuming that the light above the canopy ($I_o$) is intercepted according to Beers' law. If the potential photosynthesis rate ($P_m$), the light extinction coefficient (k) and the aerial leaf weight ($b_A$) do not vary vertically or over time, then only one factor varies during the day. We call that factor the light factor ($\gamma$). $P_{dc}$ is, in addition, reduced by a plant water reduction factor ($v_p$) which is input to the model and which varies between 0 and 1. The aerial leaf weight is about proportional to the leaf thickness and is used to bridge between the light interception per unit of leaf area and the photosynthesis per unit of leaf weight. The parameter ($I_p$) in the photosynthesis light response function is equal to the

ratio between $P_m$ and the "quantum use efficiency" at low light intensities and is almost independent of the nitrogen concentration. The maximum "potential" carbohydrate fixation per unit of leaf weight ($P_m$) is named potential although it is an increasing function of canopy nitrogen concentration ($n_l$). (Eqs. 315-317).

The incoming photosynthesis active radiation (400-700 nm) for clear sky conditions ($I_o$) is calculated hourly as a function of the solar constant ($S_o$ ; 300-3000 nm), the solar elevation (H) and a coefficient related to the air turbidity ($g_s$). The conversion from energy into quanta is made with the parameter $g_q$ (Eqs. 318-319).

For overcast conditions $P_{do}$ is calculated in exactly the same way as $P_{dc}$ (Eq. 312) but with I at the canopy top, equal to a certain fraction ($g_I$) of that for the clear sky.

$$T_{Acc} = \sum_{t=t_T}^{t_o} \text{Max}\,(T-T_1, 0) \qquad \text{if } T_{Acc} \geq T_{Sum} \text{ then growth starts} \qquad (310)$$

$$W_t' = (P_d(1-r_g)-r_m(W_s+W_r+Q_r+Q_s))T_f+W_a'(out) \qquad (*311)$$

where:

$$T_f = (T-T_1)/(T_2-T_1) \qquad \text{if } T \leq T_2 \text{ ; } \geq 0 \qquad (312)$$
$$= 1-(T-T_3)/(T_2-T_1) \qquad \text{if } T_3 < T \text{ ; } \geq 0$$
$$\text{else} = 1$$

$$P_d = P_{do}+M(P_{dc}-P_{do}) \qquad (313)$$

where:

$$M = a+bD+cD^2 \qquad (314)$$

$$P_{dc} = v_p b_A P_m \sum_{h=1}^{24} \gamma(h) \qquad (315)$$

where:

$$\gamma(h) = \frac{1}{k} \ln\left(\frac{I_o(h)+I_p}{I_o(h)\exp(-kA_{li})+I_p}\right) \qquad (316)$$

$$P_m = p_1+p_2 n_l \qquad (317)$$

$$I_o(h) = g_q S_o \sin^2 H/(\sin H+g_s) \qquad (318)$$

where:

$$S_o = 1353+45.326\cos(xt)+0.88018\cos(xt) \qquad x=2\pi/366 \qquad (319)$$
$$-0.00461\cos(xt)+1.8037\sin(xt)$$
$$+0.09746\sin(2xt)+0.18412\sin(3xt)$$

### 3.2 Allocation of biomass

*The total daily growth is allocated to structural development of roots, stems and leaves. The root growth depends on the canopy nitrogen concentration whereas the relation between stem and leaf growth is based on the balance between the leaf area and the above-ground biomass. The loss of tissues younger than one year is through roots and leaves. The roots die at a rate proportional to their growth rate whereas the leaf-fall increases towards the end of the growing season. The pool of easily available assimilates is supplied by assimilates in proportion to the total growth rate and the leaf-fall. It is used for structural growth in proportion to air temperature and the maximum daily release rate. The latter increases with stem biomass.*

The amount of assimilates allocated to roots ($W_r$') is a fraction ($b_r$) of the total daily growth ($W_t$') and the root death is a fraction ($m_r$) of the amount allocated to roots (Eq. 320).

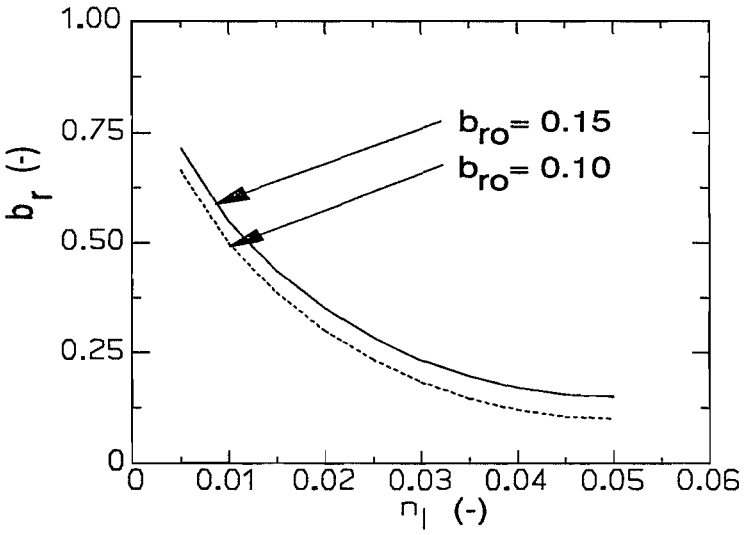



**Figure 320.** Fractional root allocation as a function of leaf nitrogen concentration. *Andelen rottillväxt som funktion av bladens kväveinnehåll.*

$b_r$ is the highest value of two functions. The first ($b_{rn}$) depends on $n_l$ and has a minimum value ($b_{ro}$) at the optimum foliage nitrogen concentration ($n_{lOpt}$) and increases as $n_l$ decreases. The second is a similar function but with the variable representing plant water status ($v_p$) as independent variable (Eqs. 321-322, Fig. 320).

The remaining part of the daily total growth ((1-$b_r$)$W_t$') is allocated to the shoots ($W_{sh}$, i.e. stems plus leaves). For the current year shoots, the stem litter can be neglected and the shoots lose biomass only through leaf-fall ($W_{lf}$'). The leaf-fall is proportional to the daily loss of leaf area ($A_{li}$'(out)) but is reduced by the fraction ($a_l$) withdrawn from leaves to plant before abscission (Eqs. 323-324).

The partitioning of the shoot growth between leaf and stem is determined by the leaf area development ($A_{li}$') which equals the difference between input ($A_{li}$'(in)) and output $A_{li}$'(out)). $A_{li}$'(out) is the leaf shedding during autumn ($A_{lia}$') which is estimated by assuming that the ratio ($m_A$) follows an empirical function over time. $m_A$ is the ratio between the leaf area of the accumulated leaf-fall ($A_{lia}$) and the sum of this leaf area and the leaf area of the canopy ($A_{li}$), and increases with time from the day of start of leaf abscission ($t_a$). The day for start of leaf abscission is determined by the daylength (after midsummer) becoming shorter and thus falling below a certain value ($d_a$). (Eqs. 325-329 and Fig. 321).

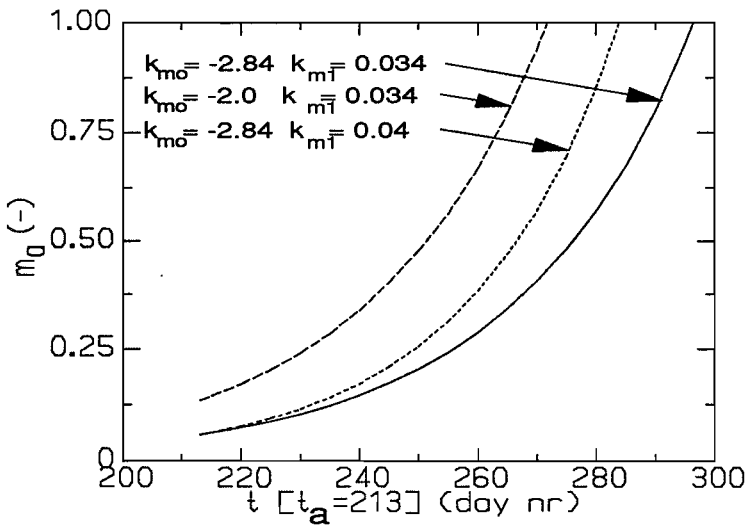



**Figure 321.** Ratio between leaf area of the falling leaves and the leaf area of all (falling and living) leaves as function of time.
*Kvoten mellan bladytan för de fallande bladen och alla (fallande och levande) blad som funktion av tiden.*

The net growth of the shoots ($W_{sh}$') is partitioned between leaves and stems in accordance with the leaf area index development ($A_{li}$') and leaf "thickness" ($b_A$). For the period before leaf abscission we assume a balance between $A_{li}$ and $W_{sh}$ to exist, expressed as the ratio $b_i$ (= $A_{li}/W_{sh}$) which decreases with plant size ($b_i = b_{io} - b_{i1}\ln(W_{sh})$) (Fig. 322). This ratio holds also for the period of leaf abscission if the leaf-fall is added to the leaf area index in the ratio $b_i$. It is necessary to restrict the leaf area increment (Ali'(in)) so that it is not higher than possible from the daily growth rate. The net leaf area change is then the difference between input and output (Eqs. 325 and 330).

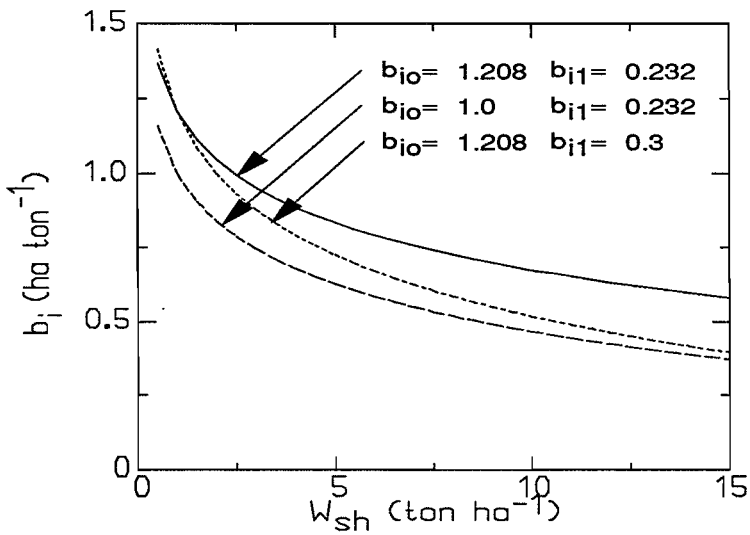



**Figure 322.** Ratio between leaf area and shoot biomass as function of shoot biomass.
*Kvoten mellan bladyta och ovanjordisk biomassa som funktion av ovanjordisk biomassa.*

The foliage biomass ($W_l$) is achieved by multiplying the new value for $A_{li}$ by $b_A$. The stem biomass ($W_s$) is simply the rest of the shoot biomass (Eqs. 331-332).

The pool in the plant with easily available assimilates ($W_a$) is filled ($W_a$'(in)) by the fraction of leaf biomass withdrawn before abscission and a fraction ($w_{ai}$) of the daily total growth. The pool is used ($W_a$'(out)) during flushing until it is empty and is not refilled during this period. The rate of release is proportional to the temperature response function ($T_f$, Eq. 312) and the maximum rate of release ($\delta W_{aMax}$) which is doubled when the total stem biomass ($W_s$+$Q_s$) equals $w_{as}$. The

temperature function relates the release of assimilates to the growth rate. If, for instance, the weather is cool and no growth occurs then no release of stored assimilates takes place (Eqs. 333-336).

| | | |
|---|---|---|
| $W_r' = (1-m_r)b_r W_t'(1-w_{ai})$ | | (*320) |
| where: | | |
| $b_r = 1+b_{ro}-(1-x^2)^{0.5}$ | $\leq 1$ | (321) |
| where: | | |
| $x = \max((n_{lMax}-n_l)/n_{lMax}) , (1-v_p))$ | $0 \leq x \leq 0.99$ | (*322) |
| $W_{sh}' = (1-b_r)W_t'(1-w_{ai})-W_{lf}'$ | | (*323) |
| where: | | |
| $W_{lf}' = (1-a_l)b_A A_{li}'(out)$ | | (324) |
| $A_{li}' = A_{li}'(in)-A_{li}'(out)$ | | (325) |
| where: | | |
| $A_{li}'(out) = A_{lia}'$ | | (326) |
| where: | | |
| $A_{lia}' = (A_{li}m_A/(1-m_A))'$ | $\geq 0$ | (327) |
| where: | | |
| $m_A = 0$ | if $t<t_a$ | (328) |
| $m_A = \exp(k_{mo}+k_{m1}(t-t_a))$ | if $t \geq t_a$ | (329) |
| $A_{li}'(in) = W_{sh}'(in)(b_{io}-b_{il}(1+\ln(W_{sh})))$ | $\leq W_{sh}'(in)/b_A$ | (330) |
| $W_l' = b_A A_{li}'$ | | (331) |
| $W_s' = W_{sh}'-W_l'$ | | (332) |
| $W_a' = W_a'(in)-W_a'(out)$ | | (*333) |
| where: | | |
| $W_a'(in) = W_{lf}'a_l+w_{ai}W_t'$ | =0 if Wa'(out)$\geq$0 | (*334) |
| $W_a'(out) = (\text{Min}(W_a , \delta W_{aMax}))T_f$ | =0 if no flushing | (*335) |
| where: | | |
| $\delta W_{aMax} = w_{ao}(1+(W_s+Q_s)/w_{as})$ | | (*336) |

# 4 NITROGEN TURNOVER SUBMODEL

## 4.1 Nitrogen available for plant uptake

*The daily growth is supplied by nitrogen from the mineral nitrogen in the soil. The uptake rate is proportional to the growth rate if there is plenty of nitrogen in the soil, otherwise it is limited by the available amount. The soil mineral nitrogen is further decreased by a fraction its contents representing the losses through leaching and denitrification. The increase of the pool is through fertilization, mineralization from litter and humus and also by a small amount leaching directly from the falling leaves. In the plant there is a pool of easily available nitrogen. However, this nitrogen is already connected to the flow of assimilates from that pool.*

The total demand for nitrogen by plant ($N_t$'(in); Eq. 412) equals the sum of the demands by the different tissues ($N_r$'(in, $N_s$'(in) and $N_l$'(in); see Eqs. 430-432). This amount is covered by nitrogen both stored in the pools of mobile nitrogen in the soil ($N_{as}$) and in the plant ($N_{ap}$) although the former is the most important (Eq. 410). In addition to this, $N_{as}$ is decreased by immobilization, leaching and denitrification. The two last terms together are considered roughly as being proportional to $N_{as}$ ($a_{ld}$). $N_{as}$ is increased by the supply of N from mineralization of litter ($N_d$(j)') and humus ($N_h$'), liquid fertilization ($N_f$', including atmospheric deposition) and leaching from the falling leaves ($N_{lfl}$'). The litter is separated into cohorts depending on its age (j). The total number of cohorts equals the age of the oldest (J) and is determined by the initial conditions, the decomposition rate and the criteria determining when the content of a decomposition cohort should be transferred to the humus pool (Eq. 411). The amount of nitrogen leached from the leaves at shedding is determined by the fraction of dry weight lost ($a_l$) and the fraction of nitrogen in that loss ($a_{ln}$; Eq. 413).

The nitrogen flows of the available pool in plant ($N_{ap}$'(in) and $N_{ap}$'(out)) strictly follow the corresponding assimilate flows (see Eqs. 333-336). Hence, this pool can cover as well as create a demand of nitrogen (Eqs. 414-416).

At flushing, an amount of nitrogen, if available, is immediately taken up by the shoot corresponding to its maximum demands (Eq. 417).

$$N_a' = N_{as}'+N_{ap}' \qquad (*410)$$

where:

$$N_{as}' = N_f'+N_{lfl}'-\sum_{j=1}^{J}(N_d(j)')-N_h'-a_{ld}N_{as}-(N_t'(in)-N_{ap}'(out)) \qquad (*411)$$

where:

$$N_t'(in) = N_r'(in) + N_s'(in) + N_l'(in) \qquad (412)$$

$$N_{lfl}' = a_{ln}a_l W_{lf}' \qquad (413)$$

$$N_{ap}' = N_{ap}'(in)-N_{ap}'(out) \qquad (*414)$$

where:

$$N_{ap}'(in) = a_l n_l W_{lf}'+w_{ai}N_t'(in) \qquad (*415)$$

$$N_{ap}'(out) = \text{Min}\,(N_t'(in)\,,\, N_{ap}) \qquad =0 \text{ if } W_a'(in)>0 \qquad (*416)$$

$$N_t'(in)(t_o) = n_{lMax}W_l(t_o)+n_{sMax}W_s(t_o) \qquad (417)$$

## 4.2 Decomposition

*All litter is assumed to be located in the soil. It is divided into compartments containing litter of equal age but a mixture as regards its origin. The litter does not start to decompose until the year after it has left the plant. The decomposition rate is determined by the activity of the microbial biomass; it increases with the soil temperature and has an optimum at a certain water content. All compartments are assumed to have the same temperature and water conditions. The activity, in relative terms, of the microorganisms decreases with litter age. The microbial biomass is assumed to be constant. After several years of decomposition the litter is transferred to the humus compartment within which the mineralization rate is lower.*

Decomposition is assumed to operate throughout the year except for days with soil temperatures below 0 °C or when the soil water factor is below a certain limit. The litter is a mixture of materials of different age, i.e of different quality, and is located from the soil surface and downwards through the soil profile. However, in the computations, the total amount of litter is distributed between cohorts, depending on age only, disregarding any variations in the tissue origin or the location of the litter. First we have the input cohort which contains the litter originating from the current year and within which no decomposition occurs. The accumulated organic matter ($W_d(o)$) and nitrogen ($N_d(o)$) in this cohort are determined by the litter fall, the nitrogen concentrations of leaves ($n_l$) and roots ($n_r$) and the fraction of N in leaves withdrawn to stems before abscission ($a_l$). The input cohort also receives litter from stems older than one year ($Q_s$ and $N_{Qs}$) which die at a daily relative rate $m_s$ (Eqs. 420-421) (cf. Eqs. 320 and 323).

There are several decomposition cohorts containing litter of one, two, three (and so forth) year-old litter, respectively. The rate of decomposition and mineralization or immobilization of nitrogen depend on the present status of the litter and on the characteristics of the microbial biomass. The microbial biomass has a constant carbon concentration ($c_m$) and efficiency ($e_o$) by which it can be produced from the assimilated litter. Its growth rate per unit of carbon in the litter (u), however, depends on the soil temperature ($T_s$) and the soil water factor ($v_s$, which is input to the model) and decreases with litter age (j). The decomposition is related to the carbon content of the litter ($C_d(o)$). Hence $W_d(o)$ is converted into $C_d(o)$ by multiplication by the litter carbon/biomass ratio ($c_l$) (Eqs. 422-424).

The microbial biomass consumes the carbon of the litter and part of this consumption increases the microbial biomass whilst the rest of it is lost through respiration. On the other hand, the litter receives carbon through death of the microbes. Assuming that the total microbial biomass remains constant all the time (i.e. growth and die-back are equal), the litter loses carbon only through microbial respiration (Eq. 425).

The nitrogen content of the litter ($N_d(j)$) is controlled by the carbon dynamics in the sense that nitrogen is lost to the microbes in accordance with their uptake of carbon from the litter (by means of $c_m$ and the actual nitrogen/carbon ratio of the litter). In turn, the litter receives nitrogen through the die-back of the microbial biomass which has a constant nitrogen concentration ($n_m$). The difference between input and output is then the mineralization or immobilization (Eq. 426).

After several years of decomposition the amount of nitrogen mineralized yearly from the cohort is negligible in comparison with the total mineralization of all cohorts. Then the content of it is transferred to the humus pool ($N_h$) for which the daily relative mineralization ($k_h$) depends on soil temperature and soil water in the same way as for the litter cohorts (Eq. 427).

| | | |
|---|---|---|
| $W_d(o)' = (1-a_l)W_{lf}'+m_rW_r'+m_sQ_s$ | | (*420) |
| $N_d(o)' = (n_l-a_{ln}a_l)W_{lf}'+n_rm_rW_r'+n_sm_sQ_s$ | | (*421) |
| $u = u_o(j)\alpha T_s v_d$ | $\geq 0$ | (*422) |
| where: | | |
| $u_o(j) = u_o(1)\beta^{j-1}$ | | (423) |
| $v_d = (v_s-a_v)/(b_v-a_v)$ | if $v_s \leq b_v$ ; $\geq 0$ | (424) |
| $= 1-(v_s-c_v)/(d_v-c_v)$ | if $v_s \geq c_v$ ; $\geq 0$ | |
| | else = 1 | |
| $C_d(j)' = -u(j)c_m(1/e_o-1)C_d(j)$ | | (425) |
| $N_d(j)' = -u(j)(c_mN_d(j)/e_o-n_mC_d(j))$ | | (426) |
| $N_h' = N_hk_h\alpha T_s$ | | (427) |

### 4.3 Plant nitrogen

*Each plant tissue grows in accordance with the relations between leaf area, shoot biomass and root biomass and the prerequisites for carbon uptake. The newly formed tissues require nitrogen in proportion to their growth. However, if the available nitrogen in soil is too small or the root uptake not efficient enough, deficiencies in nitrogen appear first in leaves, then in stems and finally also in roots. The leaves and roots lose nitrogen through litter fall.*

Nitrogen uptake by the plant is assumed to be determined by two factors: the plant's requirement for nitrogen (proportional to the daily growth) and the amount of nitrogen available for uptake ($N_a$; Eq. 430). Only a fraction ($c_u$) of the $N_a$ pool is possible to be taken up daily. This fraction can be constant or a function of root development (see section on Special functions). The uptake is limited by the smaller value of the demand and the availability. The plant reqirements depend on the maximum nitrogen concentrations in the roots ($n_{rMax}$), the stems ($n_{sMax}$) and the leaves ($n_{lMax}$) in the sense that the plant tries to supply the daily growth with nitrogen corresponding to these maximum concentrations.

The allocation of the daily total nitrogen uptake to roots ($N_r'$(in)), stems ($N_s'$(in)) and leaves ($N_l'$(in)) is based on the idea that the roots receive nitrogen first, until they reach their maximum concentrations, then the stems and finally the leaves. The plant loses biomass through the root and leaf litter whereas the stem litter is neglected (Eqs. 320, 325 and 331-332). Hence the nitrogen uptake is related to gross structural growth of roots ($W_r'$(in)=$b_rW_t'(1-w_{ai})$; see Eq. 320) and leaves ($W_l'$(in)=$b_AA_{li}'$(in); see Eq. 330) (Eqs. 430-432).

The net change in root nitrogen content ($N_r'$) is the uptake minus the amount lost through death of roots which equals the assimilates lost (last term of Eq. 320) multiplied by the nitrogen concentration of roots ($n_r$). The net change in stem nitrogen ($N_s'$) equals the uptake from the soil. Finally, the leaf nitrogen change ($N_l'$) is the uptake minus the amount lost through leaf-fall ($W_{lf}'$) to the stems and the litter pool. (Eqs. 433-435).

| | |
|---|---|
| $N_r'(in) = Min\ (c_u N_{as}\ ,\ n_{rMax} W_r'(in))$ | (430) |
| $N_s'(in) = Min\ (c_u N_{as} - N_r'(in)\ ,\ n_{sMax} W_s')$ | (431) |
| $N_l'(in) = Min\ (c_u N_{as} - N_r'(in) - N_s'(in)\ ,\ n_{lMax} W_l'(in))$ | (432) |
| | |
| $N_r' = N_r'(in) - n_r m_r b_r W_t'$ | (433) |
| $N_s' = N_s'(in)$ | (434) |
| $N_l' = N_l'(in) - n_l W_{lf}'$ | (435) |

# 5 OLD PLANT TISSUES

*The woody biomass is separated into a compartment of young tissues (<1 year old) and a compartment of older tissues (>1 year old). The older tissues have a smaller influence on growth than the younger. They affect the daily growth directly only by consuming assimilates for the maintenance respiration and by increasing the flushing rate during spring. Otherwise their effect is indirectly through the death of stems with a low nitrogen concentration which, after entering the litter pool, decreases the mineralization rate.*

Stem ($Q_s$ and $N_{Qs}$) and root ($Q_r$ and $N_{Qr}$) tissues older than one year influence the growth dynamics more indirectly than current year tissues. Stems are dying at a specific daily rate ($m_s$). The litter with a rather low nitrogen concentration is then incorporated in the input litter cohort (Eqs. 420-421) and the following year it decreases the mineralization rate. Concerning the roots, only the current year-old roots are assumed to die-off (Eq. 320). Both old stem and root biomass consume energy for maintenance respiration which is taken directly from the daily assimilation (Eq. 311). The old stem biomass also influences the rate of flushing (Eq. 336). At the end of each year the current year growths of stem and root are transferred to the older tissues compartments and thereafter initialized for the next year. If there are any leaves left at this time they are moved to the litter pool (Eqs. 500-503).

| | | |
|---|---|---|
| $Q_s' = -m_s Q_s$ | daily | (*500) |
| $= W_s$ | yearly | |
| | | |
| $N_{Qs}' = -m_s N_{Qs}$ | daily | (*501) |
| $= N_s$ | yearly | |
| | | |
| $Q_r' = W_r$ | yearly | (502) |
| $N_{Qr}' = N_r$ | yearly | (503) |

# 6 HARVEST

*This option is formulated in a general way to enable simulation of different kinds of reductions in growing tissues. The term harvest is used although it generally implies the reduction of growing tissues. The disturbance starts the flushing, and the plant develops in a way similar to that after budbreak during spring. The plant then uses the easily available pool in the plant which, however, was reduced by the harvest. The growing tissues lost by the plant either leave the system (i.e. harvest) or enter the ground.*

The stand can be harvested at any day ($t_h$) of the year. The leaf biomass ($W_l$), stem biomass of the current year ($W_s$) and stem biomass older than one year ($Q_s$) can be reduced separately by the fractions $d_l$, $d_s$ and $d_Q$, respectively (Eqs. 600-602). (Roots can be reduced in the same proportion as the stems by setting a negative value for $d_s$ or $d_Q$.)

Of the amount reduced, a certain fraction ($h_l$, $h_s$ and $h_Q$, respectively) is taken out of the plantation (Eqs. 603-605) whereas the rest is transferred to the litter pool ($W_d(o)$ and $N_d(o)$) (Eqs. 606-607). The nitrogen contents are changed in the same proportions as the biomass. The growth starts again after harvest according to the growth and allocation functions used for normal growth.

The easily available pool of assimilates ($W_a$) and nitrogen ($N_{ap}$) in the plant are assumed to be located in the stems and roots in proportion to their biomass. Hence, the reduction in $W_a$ and $N_{ap}$ depends on the fraction of stems removed in relation to total root and stem biomass before harvest (Eqs. 608-609).

The roots can also be reduced although they are not presented in the formulas below. By giving the parameters $d_s$ and $d_Q$ negative values the roots are handled in the same way as the stems.

$$W_l = (1-h_l)W_l \quad (600)$$
$$W_s = (1-h_s)W_s \quad (*601)$$
$$Q_s = (1-h_Q)Q_s \quad (*602)$$

$$N_l = (1-h_l)N_l \quad (603)$$
$$N_s = (1-h_s)N_s \quad (*604)$$
$$N_{Qs} = (1-h_Q)N_{Qs} \quad (*605)$$

$$W_d(o) = (1-h_l)d_lW_l+(1-h_s)d_sW_s+(1-h_Q)d_QQ_s \quad (*606)$$
$$N_d(o) = (1-h_l)d_lN_l+(1-h_s)d_sN_s+(1-h_Q)d_QN_{Qs} \quad (*607)$$

$$W_a = W_a((1-d_s)W_s+(1-d_Q)Q_s)/(W_s+Q_s+W_r+Q_r) \quad (*608)$$
$$N_{ap} = N_{ap}((1-d_s)W_s+(1-d_Q)Q_s)/(W_s+Q_s+W_r+Q_r) \quad (*609)$$

# 7 SPECIAL FUNCTIONS

Here five functions are presented that normally not are used in the simulations. They represent both alternative and complementary hypotheses to those of the original model. They are activated by changing the appropriate sensitivity or start parameters. The options are as follows: (i) The light extinction coefficient varies with depth in the canopy, instead of constant; (ii) the leaf-fall is increased by an amount determined by the light conditions in the canopy; (iii) the leaf "thickness" varies with the age of the stems, instead of being independent of age; (iv) the nitrogen uptake can be a function of root activity and size, and (v) the stand is split up into single trees which are simulated individually, but which compete for light and nitrogen.

## 7.1 Different functions

The daily carbohydrate fixation for the whole canopy ($P_{dc}$ ; see Eqs. 315-316) can be estimated using a light extinction coefficient ($k_i$) that varies with depth in the canopy. This is done by summing, starting from the top, the light coefficient ($\gamma_i$) for layers (i) with a leaf area index of $\delta A$. The light above the layer concerned ($I_i$) is intercepted according to the light extinction coefficient of that layer ($k_i$) which is a function of the leaf area index accumulated from above ($A_i$) (Eqs. 710-712).

The loss rate of leaf area ($A_{li}$'(out)) is put equal to the leaf shedding during autumn ($A_{lia}$') in the basic version of the model (see Eq. 326). However, we can add to this the leaf-fall caused by self-shading ($A_{liI}$'). In this case, the leaves are assumed to fall when their net photosynthesis is negative, i.e. when the light at their level in the canopy is below the compensation point ($I_d$). The light variable chosen to be compared with $I_d$ is the daily mean of incident light inside the canopy ($I_{i-1}$) at clear sky conditions (clear sky conditions are chosen here since the actual light values are never calculated, see Eqs. 311-312). Above the level where $I_{i-1}$ equals $I_d$ the leaf area index equals $A_{lix}$, whilst the leaves in that layer or below it fall to the ground (Eqs. 713-714).

The "leaf thickness" could be put equal to a function that increases with shoot-age. Then, $b_A$ increases each year (j) by a fraction $b_{A1}$ (Eq. 715).

The fraction of the mineral nitrogen in the soil that can be taken up by roots is constant in the model ($c_u$, Eqs. 430-432). However, assuming this fraction to be related to the root development we can set it proportional ($c_{u1}$, $c_{u2}$ and $c_{u3}$) to the daily root growth ($W_r$'), the root biomass not older than one year ($W_r$) and the root biomass older than one year ($Q_r$). (Eq. 716).

$$P_{dc} = v_p b_A P_m \sum_{h=1}^{24} \left( \sum_{i=1}^{A_{li}} \gamma_i(h) \right) \qquad (710)$$

where:

$$\gamma_i(h) = \frac{1}{k_i} \ln\left(\frac{I_i(h)+I_p}{I_i(h)\exp(-k_i\delta A)+I_p}\right) \qquad (711)$$

where:

$$k_i = a+b(A_i-\delta A/2)+c(A_i-\delta A/2)^2 \qquad (712)$$

$$A_{liI}' = A_{li}-A_{lix} \qquad \geq 0 \qquad (*713)$$

where:

$$A_{lix} = A_{li}\frac{I_d/I_{i-1}-\exp(-k_i)}{1-\exp(-k_i)} \qquad (*714)$$

$$b_A = b_{Ao}(1+b_{A1}j) \qquad (715)$$

$$c_u = c_{u1}W_r'+c_{u2}W_r+c_{u3}Q_r \qquad c_u \leq c_{uMax} \qquad (*716)$$

## 7.2 Competition between plants

*Assuming that the functions of the stand model described above are the same for single plants we simulate the production of single plants by running the model several times during each time step. By using the individual light and nitrogen availability for each plant we simulate the effect on growth of the competition for light and nitrogen among plants. The plants have different abilities to take up nitrogen and receive light as a consequence of different sizes at the beginning of the growing season. The plants selected for the calculations should be neighbours and randomly distributed over the area concerned as regards plant size. Moreover, it is assumed that all plants have the lower edge of their canopy at the same level. Then all differences between plants in this respect are located to the upper layers of the canopy.*

The source for the appearance of competition between plants are the differences in assimilates available for flushing stored in the plant ($W_a$). At the time for the start of the seasonal growth, differences in development of leaves, stems and roots then appear. The plant with a large root biomass extracts more nitrogen from the pool of nitrogen in the soil ($N_{as}$ ; see Eq. 411) than the one with a small root biomass. The availability of nitrogen for the single plant ($N_{as}(l)$) is proportional to the ratio between its root biomass ($W_r(l)$) and the mean root biomass of all plants ($W_r$). (Eq. 720)

The larger plants are shading the smaller plants which then receive less light for photosynthesis. It is assumed that the lower edge of the canopy does not differ between plants and that the leaves of the whole canopy (i.e. of all plants) are, at each level in the canopy, uniformly distributed over the ground surface. The canopy leaf area index ($A_{li}$) then equals the average leaf area index of all single plants ($A_{li}(l)$). In the canopy there are layers containing leaves belonging to a different number of plants. At the top, only the highest plant (or plants) is present while at the bottom there are leaves from all plants.

For each layer in the canopy the photosynthesis of the single plant is proportional to the light factor of that plant in that layer ($\gamma_i(l)$) (see Eq. 710). This factor is determined by first calculating the average light factor for all plants in the layer ($\gamma_i$) using Eq. 711 together with the average leaf area index of the layer ($\delta A_i$). The light factor of the single plant $\gamma_i(l)$ is then calculated by sharing the average light factor between the plants in the layer. This is done by multiplying it by, the number of plants contributing with leaves to the layer ($l_i$) divided by the total number of plants in the whole group ($l_{Max}$). If the plant does not reach up to layer i then its light factor is zero (Eq. 721).

The leaf area index of the highest layer ($\delta A_1$) equals the difference (> 0) between the highest (one or several plants) and the next highest (one or several plants) leaf area index of single plants ($A_{li}(l)$). For the second highest layer $\delta A_2$ is determined in a similar way, being the difference between the second and the third levels of leaf area indices, and so on for successively deeper layers.

$$N_{as}(l) = N_{as} W_r(l)/W_r \qquad (*720)$$

$$\gamma_i(l) = l_{Max}/l_i \gamma_i \qquad =0 \text{ if } A_{li}(l) < A_{li} - \Sigma\delta A_i \qquad (*721)$$

# 8 SIMULATION EXAMPLE

A simulation of the growth of a *Salix viminalis* stand (clone 683; site area is 2.7 ha) on an agricultural soil at Uppsala (Sweden) is used as an example of how to use the model (concerning site description see Verwijst, 1991). The simulation was made for a four-year period (1985 to 1988). As far as possible, the same input variables and parameter values were used as did Eckersten (1991b) who made a similar simulation for the same stand but using another model (SOILN-FORESTSR, cf. Eckersten & Jansson, 1991; Johnsson *et al.*, 1987). The two models differ as regards the soil "submodel" included. Therefore, only some of the parameters related to the soil processes were similar. The climatic driving variables related to the air were taken from a station at the Swedish University of Agricultural Sciences located 1 km west of the stand, whereas those related to the soil were provided by a soil heat and water model named SOIL (Jansson 1991). The simulation with the SOIL model was based on the parameterization and simulations made by Persson & Lindroth (1991) for the same stand and during the same four-year period (however, only during the vegetation periods). The fertilization regime was prepared by Tom Ericsson (unpublished data, 1991).

The parameter values were the same as used by Eckersten & Slapokas (1990) for *S. viminalis* (clone 082) at Studsvik (Sweden). However, the photosynthesis parameters ($P_m(a)$, $P_m(b)$ and $p_l$) were changed in accordance with laboratory measurements on clone 683, the leaf "thickness" ($b_A$) was given a constant value about equal to that observed on the stand and the turbidity coefficient ($g_s$) was decreased with 20% in accordance with the less maritime climate at Uppsala. The fact that the root system became established during the simulation period (especially during 1985) made it important to choose appropriate values of the parameters used for determining the fraction ($c_u$) of the total soil mineral nitrogen ($N_{as}$) actually available for daily root uptake (Eqs. 430-432 and 716). It was assumed that an established root system of 2 ton DW $ha^{-1}$ could take up 8% of $N_{as}$ and that $c_u$ increased linearly with total root biomass up to this value. The stand did not follow "normal" growth during the simulation period. It was harvested and disturbed by a fungi attack. Therefore some parameters were changed during the simulation in accordance with these events. The fungi attack during 1987 was considered by reducing the photosynthetic rate so as to fit (roughly) the simulated stem biomass to the measured one at the end of that year.

## 8.1 Input

The stand was planted during the summer 1984 and at start of the growth simulation (1985-01-01) the plant had an initial biomass and the soil contained a certain amount of mineral nitrogen. The contents of litter cohorts older than one year were derived by the model from the initial value of the one-year-old decomposition cohort and the parameter for the length of the earlier decomposition periods ($t_{Dec}$). Initial values of state variables are given in Table 811 and parameter values at start of simulation in Table 810.

**Table 810.** Parameter values at start of simulation. Explanations of symbols and units are given in the List of symbols. *Parameter värden vid start av simuleringen.*

| Parameter | Value | Parameter | Value | Parameter | Value |
|---|---|---|---|---|---|
| START | | | | | |
| Latitude | 59.8 | | | | |
| $b_A$ | 65.0 | | | | |
| $t_{Dec}$ | 210 | | | | |
| PHOTOSYNTHESIS | | | | | |
| $I_d$ | 10.0 | | | | |
| k(a) | 1.1050 | k(b) | -0.007338 | k(c) | -0.02376 |
| $P_m$(a) | 18.06* | $P_m$(b) | 9.65* | $p_I$ | 380 |
| $g_s$ | 0.25 | $g_q$ | 2.3 | $g_I$ | 0.3 |
| $g_h$ | 0.920 | | | | |
| M(a) | -0.7E-02 | M(b) | 1.68 | M(c) | -0.657 |
| $r_g$ | 0.25 | | | | |
| δA | 1.0 | | | | |
| C-ALLOCATION | | | | | |
| $m_r$ | 0.5 | $m_s$ | 0.0002 | | |
| $w_{as}$ | 0.1E+07 | $w_{ai}$ | 0.03 | $w_{ao}$ | 40.0 |
| $b_{ro}$ | 0.150 | | | | |
| $b_{io}$ | 1.21 | $b_{il}$ | 0.232 | | |
| $k_{m1}$ | 0.340E-01 | $k_{mo}$ | -2.84 | $d_a$ | 15.5 |
| N-ALLOCATION | | | | | |
| $n_{lMax}$ | 5 | $n_{rMax}$ | 3 | $n_{sMax}$ | 0.5 |
| N-AVAILABILITY | | | | | |
| $a_d$ | 0.0 | $a_{id}$ | 0.001 | $a_w$ | 0.25 |
| $c_{uMax}$ | 0.08 | $c_{u2}$ | 0.00004 | $c_{u3}$ | 0.00004 |
| DECOMPOSITION | | | | | |
| $e_o$ | 0.410 | $u_o$(1) | 0.01575 | | |
| $c_m$ | 0.5 | $n_m$ | 0.1 | $c_l$ | 0.5 |
| β | 0.4 | α | 0.1 | | |
| $k_h$ | 0.000023 | | | | |
| $a_{ln}$ | 0.005 | $a_l$ | 0.2 | | |
| TEMPERATURE, ETC. | | | | | |
| $T_1$ | 5.0 | $T_2$ | 5.0 | $T_3$ | 25.0 |
| $r_m$ | 0.0001 | | | | |
| $t_T$ | 60.0 | $T_{Acc}$ | 40.0 | | |
| WATER | | | | | |
| $a_v$ | 0.3 | $b_v$ | 0.4 | | |
| $c_v$ | 0.7 | $d_v$ | 0.8 | | |

CHANGES of parameter values during the simulation period:

| | | | | | |
|---|---|---|---|---|---|
| 1987-02-01: | All stem biomass was harvested and removed from the plantation. | | | | |
| $t_h$ (day number) | 32.0 | $d_Q$ | 0.999 | $h_Q$ | 1 |
| 1987-07-01: | The canopy leaves were attacked by fungi. The attack is assumed to have caused a decrease in the photosynthesis rate by 80%. | | | | |
| $P_m$(a) | 4.5* | $P_m$(b) | 2.4* | | |
| 1988-02-01: | The leaves of the new shoots were healthy. Hence the photosynthesis rate achieved normal values again. No harvest was taken this year. | | | | |
| $P_m$(a) | 18.06* | $P_m$(b) | 9.65* | $t_h$ | 0. |

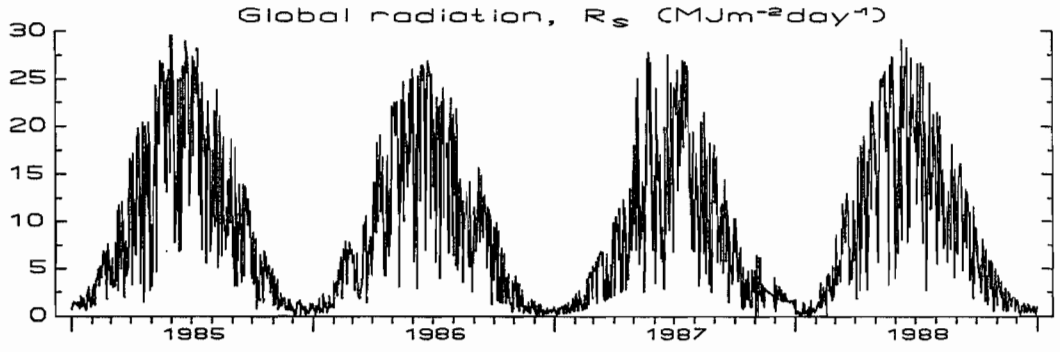
*) Unit is $mgCO_2\ gDW^{-1}\ h^{-1}$

**Table 811.** Initial values of state variables 1 January 1985. Explanations of symbols are given in the list of symbols. *Initiala värden på tillståndsvariabler 1 januari 1985.*

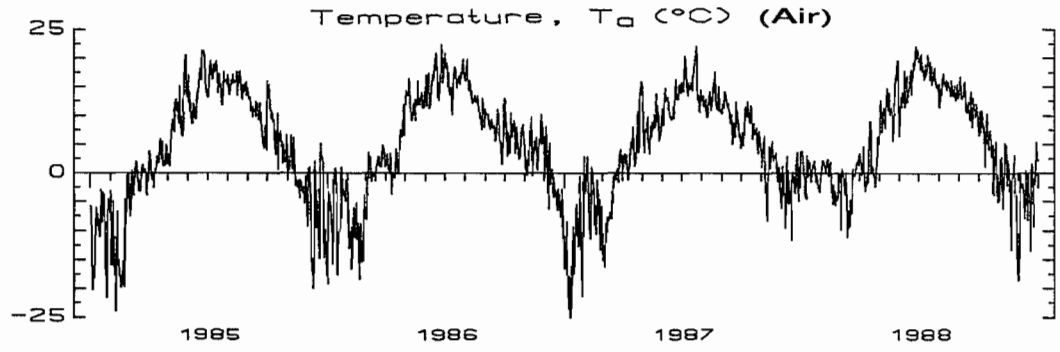
| Biomass | kgDW ha$^{-1}$ | Nitrogen | kgN ha$^{-1}$ |
|---|---|---|---|
| $W_r$ | 1.0 | $N_r$ | 0.03 |
| $Q_r$ | 600 | $N_{Qr}$ | 18 |
| $Q_s$ | 600 | $N_{Qs}$ | 3 |
| $W_a$ | 100 | $N_a$ | 50 |
| $W_d(1)$ | 3660 | $N_d(1)$ | 124 |
| $W_h$ | 3500000 | $N_h$ | 7000 |

The input variables were daily values of global radiation, mean air temperature at reference height, mean soil temperature at 20 cm depth, plant water reduction factor (i.e. actual/potential evapotranspiration ratio), soil relative water content at 20 cm depth and liquid N-fertilization. The plant water factor and soil heat and water variables were provided by the SOIL model (Persson & Lindroth, 1991) (Figs. 810a-f).

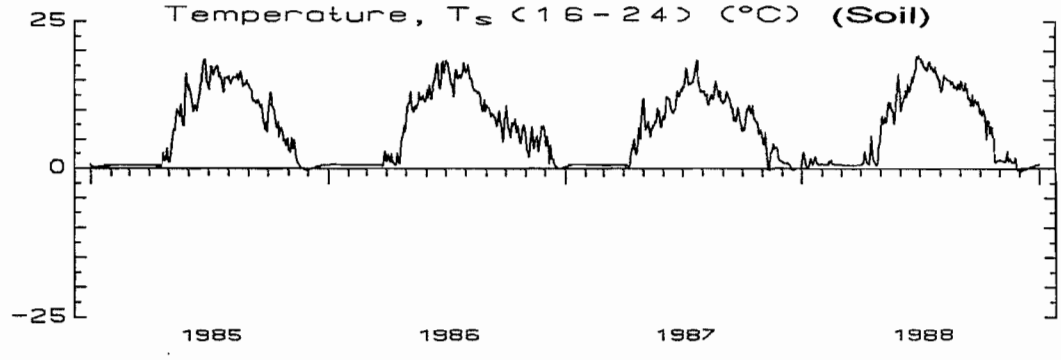
**a**



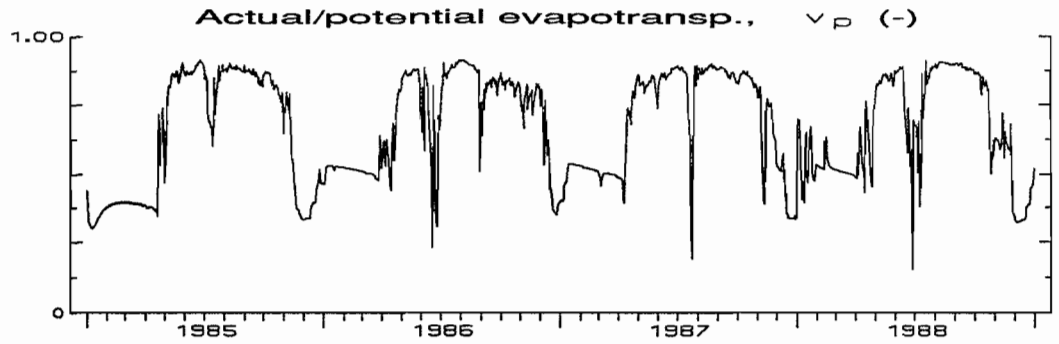

**b**



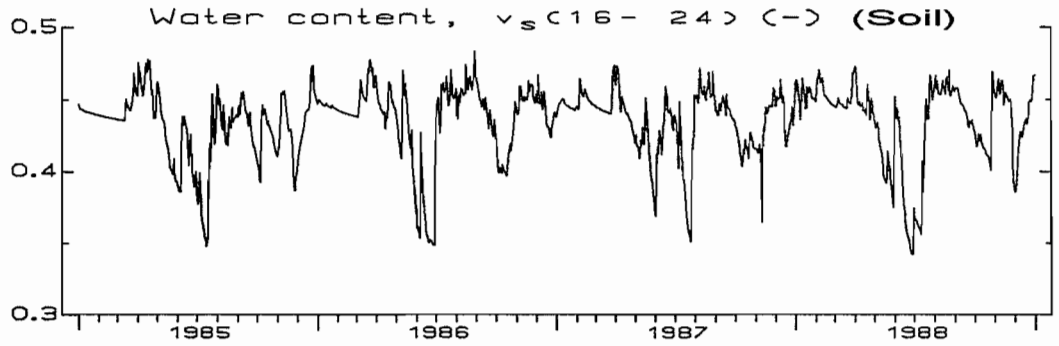

**c**



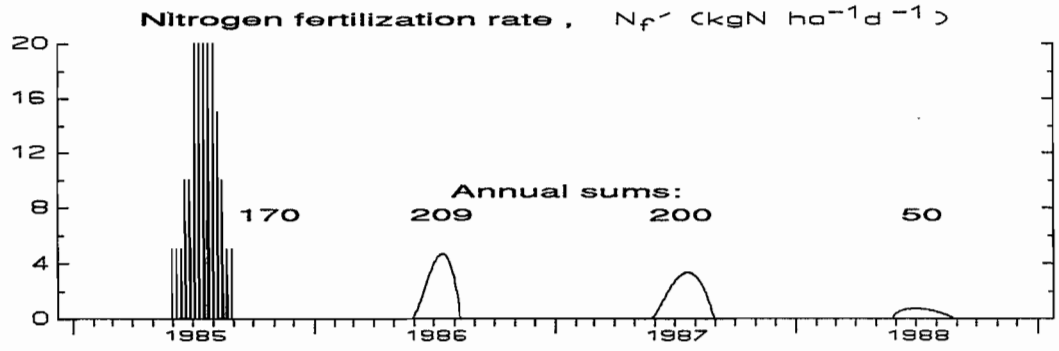
d




e




f




**Figures 810a-f.** Input variables of the simulation. *Drivvariabler till simuleringen.*

## 8.2 Output

In a special output file (WIGO.AUT) the program presents some annual values of accumulated flows, and some state variables (Table 820)

**Table 820.** Annual values of accumulated flows (') and states at the end of the year (in units of kg $ha^{-1}$, otherwise noted). For explanation of symbols see List of symbols. *Ackumulerade flöden (årsvis) (') samt tillståndsvariabler vid årets slut (kg $ha^{-1}$ om inte annat angivits).*

| Variable | $W_t$'(in) | $W_{sh}$'(in) | $W_{sh}$'(out) | $W_r$'(in) | $W_r$'(out) | $W_d$(o) |
|---|---|---|---|---|---|---|
| Year | (ton $ha^{-1}$) | (ton $ha^{-1}$) | (ton $ha^{-1}$) | (ton $ha^{-1}$) | (ton $ha^{-1}$) | (ton $ha^{-1}$) |
| 1985 | 15.7 | 11.8 | 3.5 | 3.7 | 1.9 | 4.7 |
| 1986 | 20.5 | 16.5 | 4.3 | 3.9 | 1.9 | 5.7 |
| 1987 | 8.8 | 7.4 | 2.5 | 1.4 | 0.7 | 2.7 |
| 1988 | 26.6 | 22.0 | 5.1 | 4.5 | 2.2 | 6.6 |

| Variable | $N_l$'(in) | $N_l$'(out) | $N_s$'(in) | $N_r$'(in) | $N_r$'(out) |
|---|---|---|---|---|---|
| Year | | | | | |
| 1985 | 176 | 178 | 40 | 112 | 56 |
| 1986 | 225 | 227 | 58 | 117 | 58 |
| 1987 | 161 | 163 | 23 | 42 | 21 |
| 1988 | 322 | 334 | 81 | 135 | 67 |

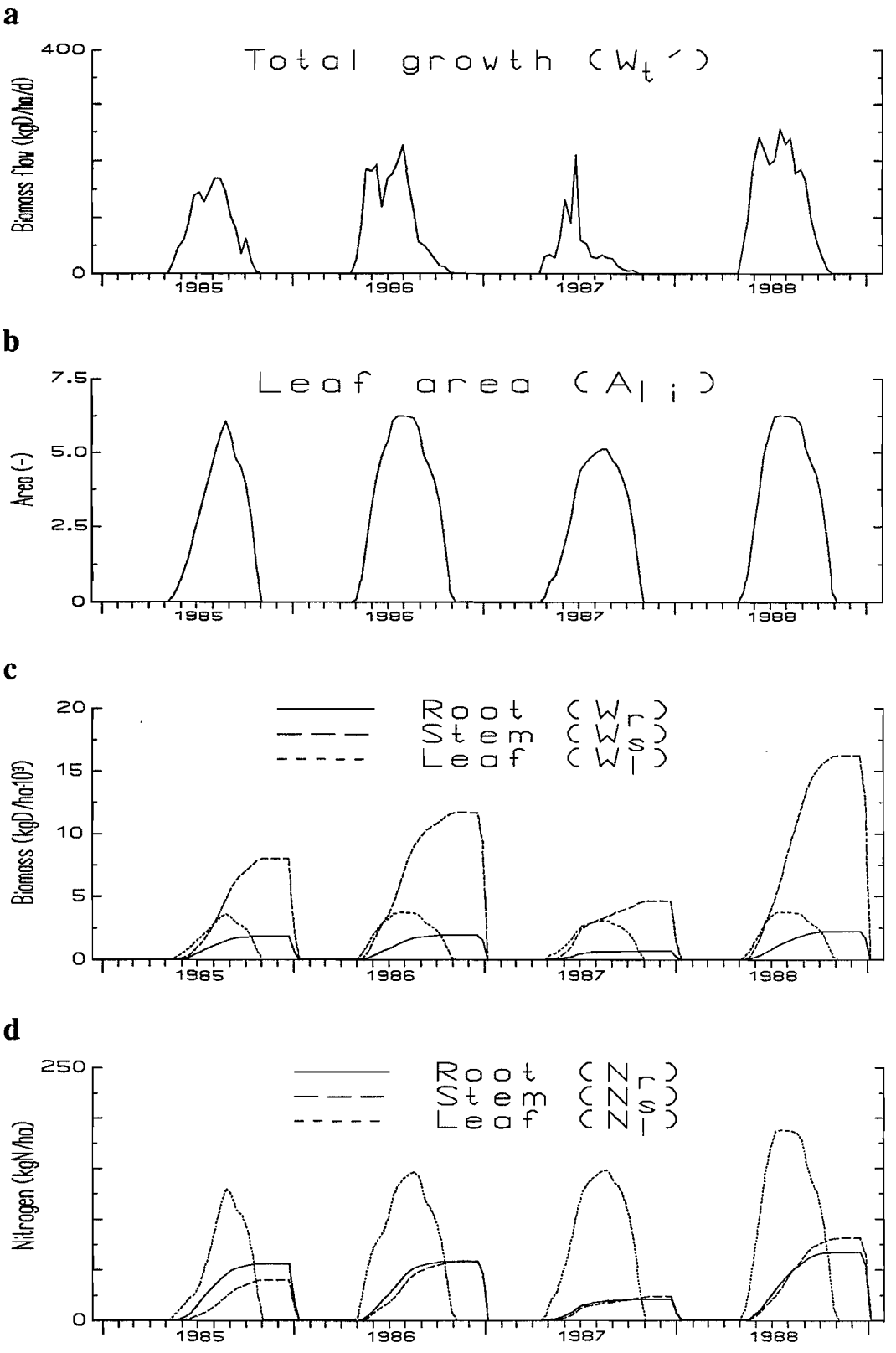
| Variable | $N_d$(o) | $\Sigma N_d$(j)'(out) | $N_h$'(in) | $N_h$'(out) | $N_f$' |
|---|---|---|---|---|---|
| Year | | | | | |
| 1985 | 186 | 122 | 0 | 35 | 170 |
| 1986 | 226 | 180 | 0 | 38 | 209 |
| 1987 | 141 | 206 | 0 | 35 | 200 |
| 1988 | 312 | 153 | 0 | 36 | 50 |

| Variable | $N_{ap}$'(in) | $N_{ap}$'(out)* | $N_{ap}$ | $N_{as}$ | $W_a$ |
|---|---|---|---|---|---|
| Year | | | | | (ton $ha^{-1}$) |
| 1985 | 54 | 0 | 54 | 36 | 1.6 |
| 1986 | 69 | 57 | 65 | 100 | 1.8 |
| 1987 | 48 | 12 | 46 | 269 | 1.0 |
| 1988 | 100 | 48 | 96 | 4 | 2.3 |

| Variable | $N_{lfl}$' | $W_h$'(in) | $\Sigma N_d$(j) | $\Sigma W_d$(j) |
|---|---|---|---|---|
| Year | | | | |
| 1985 | 4 | 0 | 67 | 730 |
| 1986 | 4 | 0 | 74 | 786 |
| 1987 | 3 | 0 | 93 | 1001 |
| 1988 | 5 | 0 | 81 | 852 |

*) harvest not included

Output variables are given every 10 days. The daily total growth and the leaf area index are shown in Figs. 820a-b. The accumulated structural growths of the current year for roots, stems and leaves are shown in Fig. 820c and the corresponding nitrogen contents in Fig. 820d.



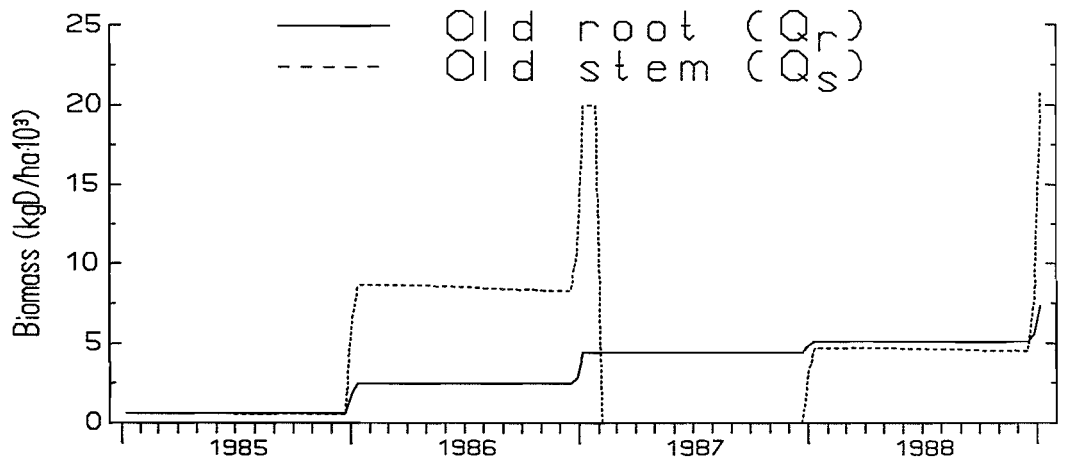

**Figures 820a-d.** Output variables on total growth and accumulated growth during the current year. For explanation of symbols see List of symbols. *Utdata för daglig tillväxt och ackumulerad tillväxt under året.*

The accumulated values of stem and root biomass older than one year and the corresponding nitrogen contents. The harvest and damage simulated in 1987 and 1988 are visible as sudden reductions in these values (Figs. 821a-b).

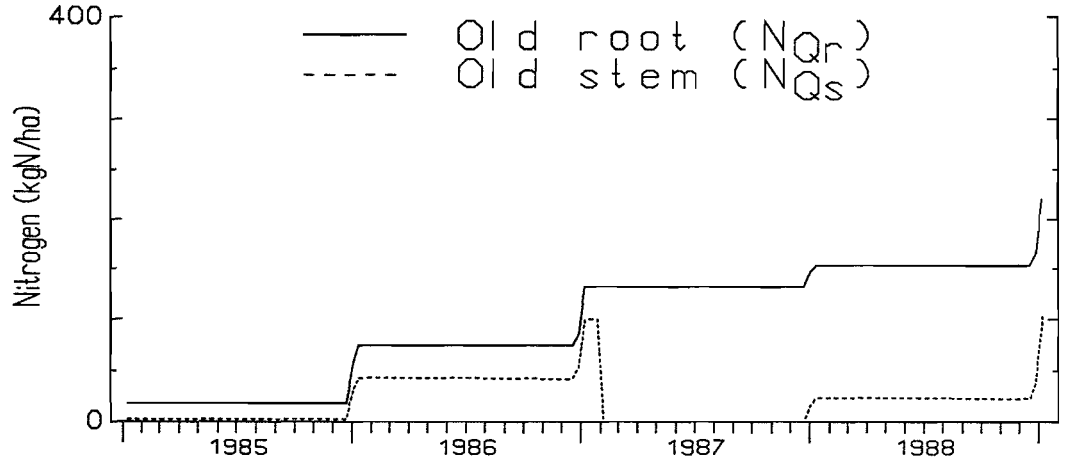
These reductions due to harvest and damage are also visible in the pool of easily available assimilates in the plant (Fig. 822a). The amount of nitrogen in this pool is not small in comparison with the mineral nitrogen pool of the soil (Fig. 822b).

The litter falls into a litter cohort within which no decomposition occurs (Fig. 823a). At the end of the year this litter is transferred to the youngest decomposition cohort, the nitrogen content of which is shown in Fig. 823b together with the total amount in all cohorts. The total daily mineralization from all cohorts (Figs. 824a-b) mainly originates from the youngest.

**a**

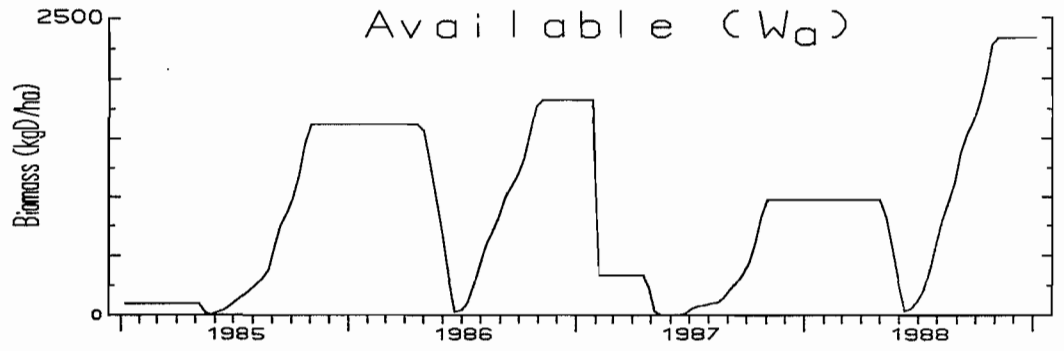



**b**

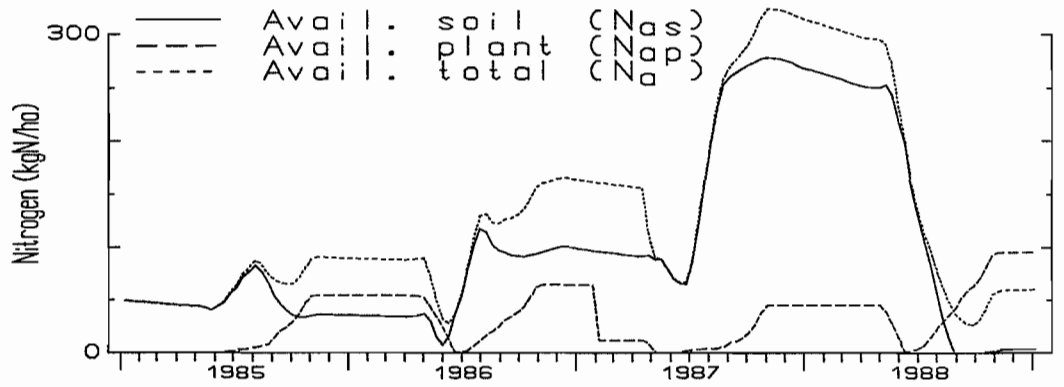



**Figures 821a-b.** Output variables on biomass and nitrogen content of tissues older than one year. For explanation of symbols see List of symbols. *Utdata för biomassa och kväveinnehåll i vävnader äldre än ett år.*

a

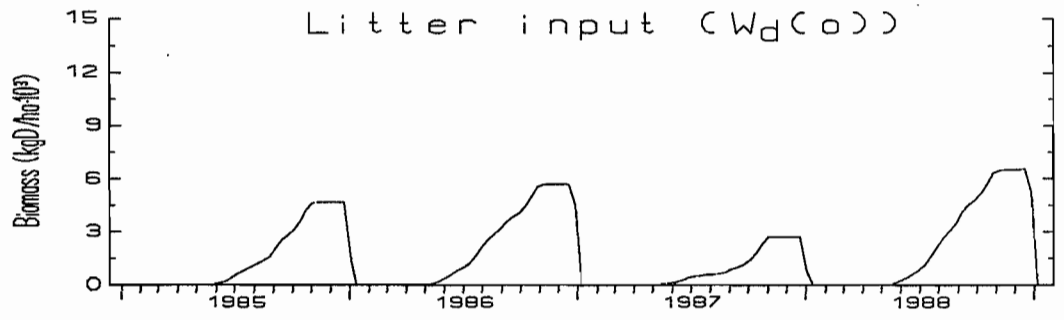



b

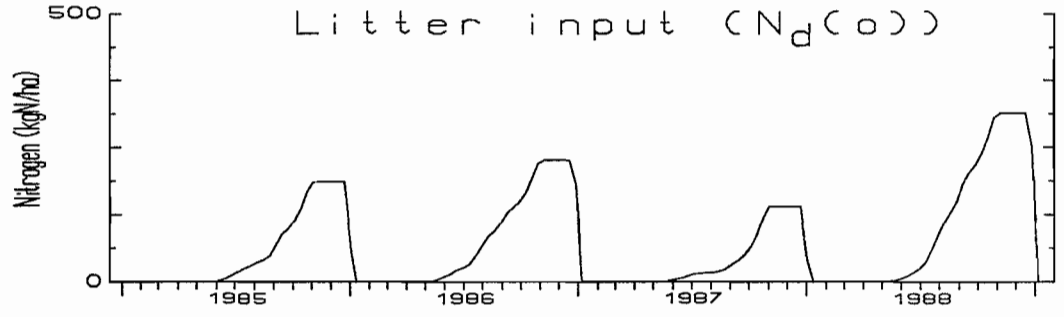



**Figures 822a-b.** Output data on available pools of assimilates and nitrogen. For explanation of symbols see List of symbols. *Utdata för tillgängliga pooler av assimilat och kväve.*

a

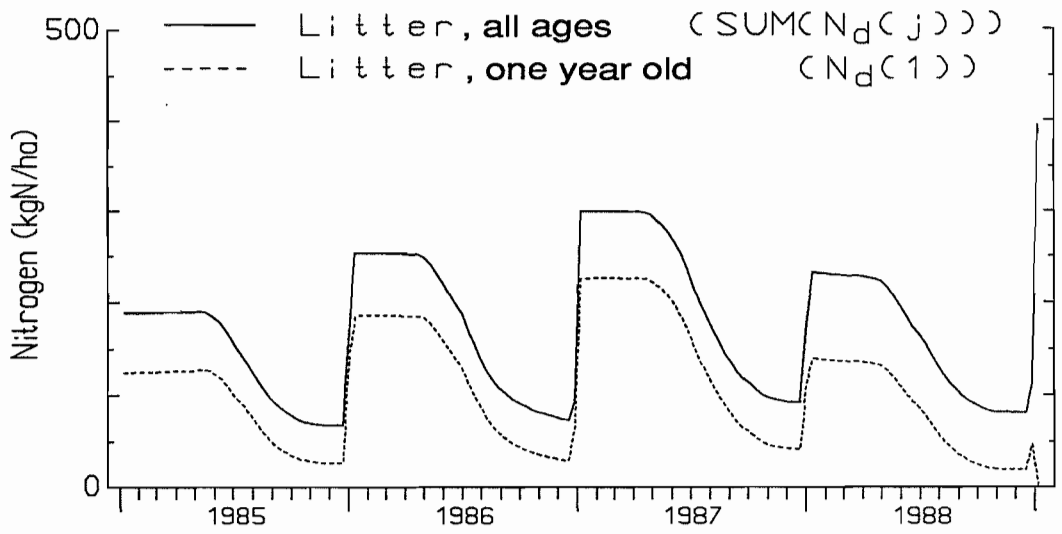



b

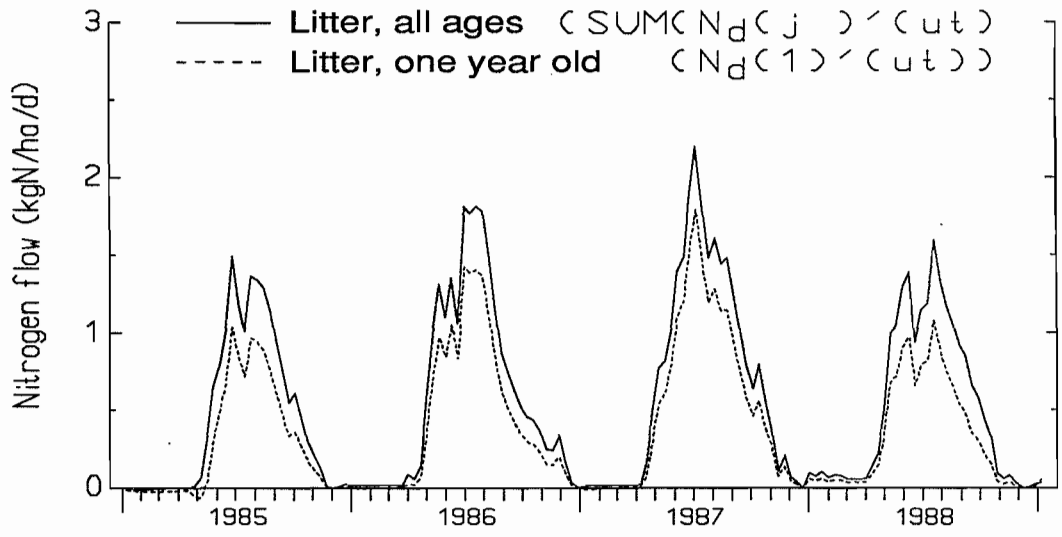



**Figures 823a-b.** Output data on biomass and nitrogen content of accumulated litter fall. For explanation of symbols see List of symbols. *Utdata för biomassa och kväveinnehåll i förnafall.*

**a**




**b**

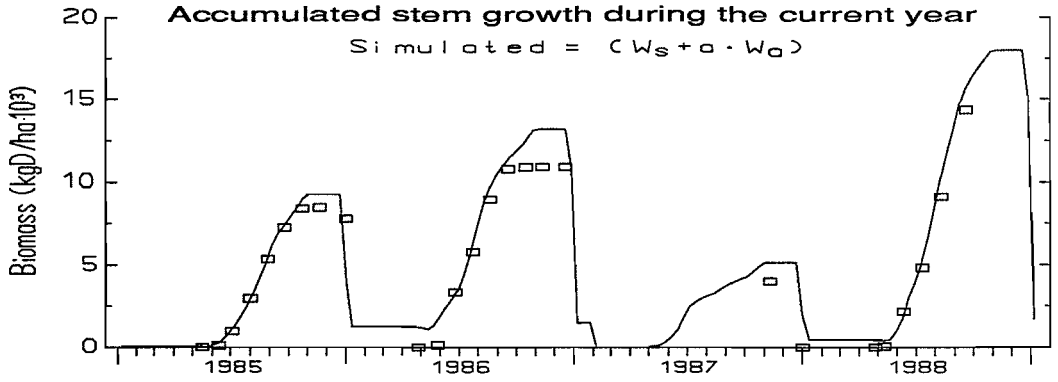



**Figures 824a-b.** Output data on nitrogen contents of decomposing litter and mineralization rates. For explanation of symbols see List of symbols. *Utdata för kväveinnehåll i förna som håller på att brytas ned samt mineraliseringshastigheter.*

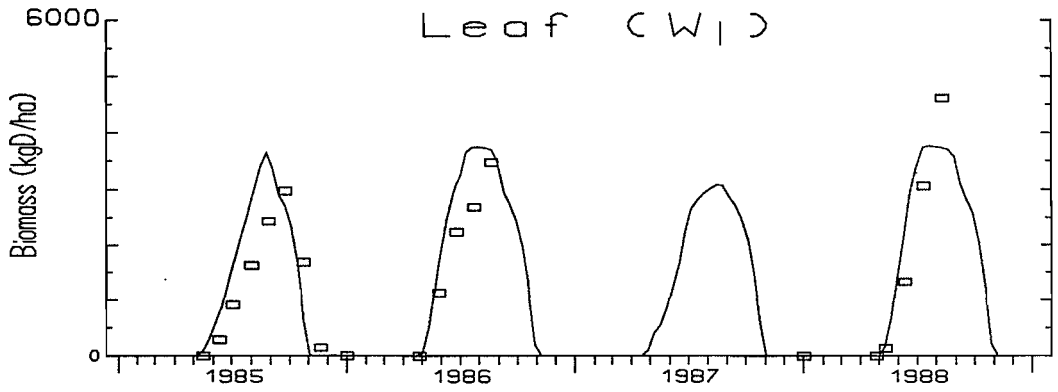
## 8.3 Validation

The simulation made above was compared with measured data on stem biomass, leaf biomass, accumulated leaf-fall, leaf area and mineral soil nitrogen down to 90 cm depth (Tom Ericsson, Theo Verwijst and Lars-Owe Nilsson, unpublished data, 1991; see also Eckersten 1991b). The measured stem biomass includes both the structural growth and available assimilates. To compare the simulations with the measurements the simulated structural growth was supplemented by a fraction of the assimilates in the easily available pool. This fraction (a) was taken equal to the ratio between stem biomass and total biomass (Figs. 830a-g).

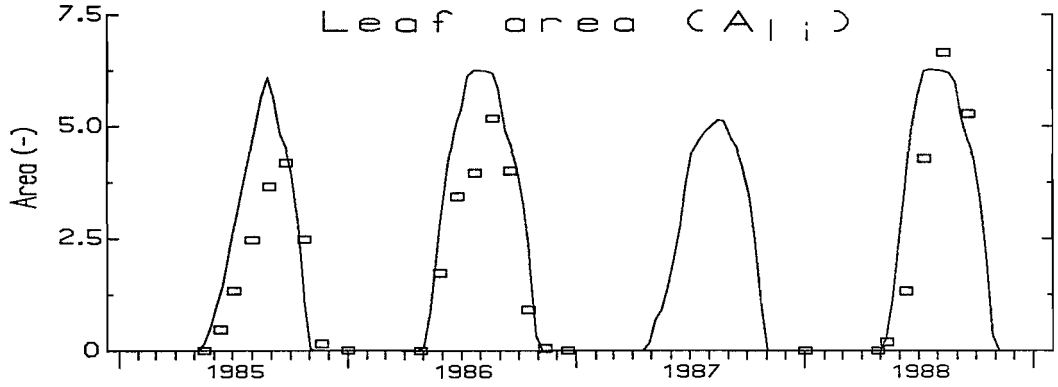
**a**

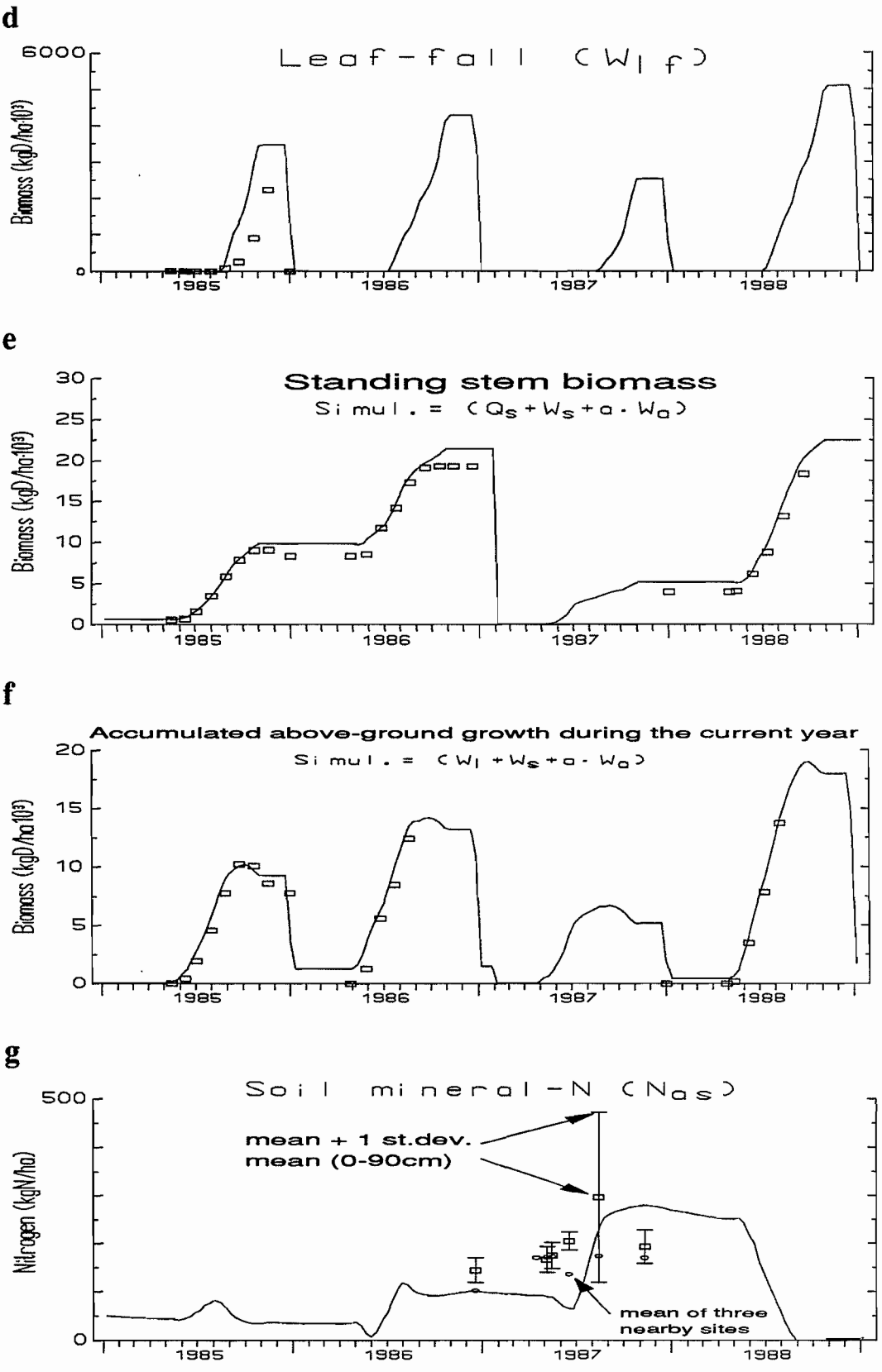



**b**




**c**






**Figures 830a-g.** Comparison between simulated (lines) and measured (points) data. g) The soil mineral nitrogen is a mean of 4 subareas comprising the whole site. The nearby sites are much smaller (150 $m^2$) than the experimental site. For explanation of symbols see List of symbols. *Jämförelse mellan simulerade (linjer) och uppmätta (punkter) data.*

During the first year the ratio between leaf and stem biomass was overestimated (Figs. 830a and b), however, the above-ground biomass was fairly well simulated (Fig. 830f). The stem production is overestimated at the end of the season (Fig. 830a). A large fraction of the assimilates withdrawn from leaves before abscission is allocated to the stems in the simulation. Perhaps this fraction is overestimated and more should be allocated to roots. The soil mineral nitrogen seems to be underestimated (Fig. 830g) either because of too high plant uptake or too low mineralization rate or both. Both measurements and simulation show a large increase in soil mineral nitrogen during 1987.

A regression analysis comparing simulated and measured values showed that the model simulated the stem biomass with good accuracy (high $R^2$-values in Table 830); however with a systematic overestimate of low values ($a<0$ in Table 830) that is further increased for high values ($b<1$ in Table 830). Leaf biomass was less accurately simulated. The simulated periodic changes (i.e. the changes occurring between two successive measuring occasions) showed lower correlations (values in brackets in Table 830). This is, especially concerning the leaf biomass, partly because the simulated state of the plant at the start of the period was not adjusted to the measured state. The following values were excluded in the regressions: all measurements when the daily average temperature was below 5 °C, leaf-fall measurements equal to zero and the stem biomass measurement of 1987. The correlations for soil mineral nitrogen are very poor either because the measurements are few and uncertain or the simulations are incorrect or both.

**Table 830.** Comparison of simulated and measured values at Uppsala using regression analysis. The regression equation used was as follows: Measured value = a + b·Simulated value. Values in brackets refer to changes that occur between samplings. *Jämförelse mellan simulerade och mätta värden m.h.a. regressionsanalys. Följande regressionsekvation användes: Mätvärde = a + b.Simulerat värde. Värden inom parantes avser ändringar mellan mättillfällen.*

| Variable | $R^2$ (-) | a (kg $ha^{-1}$) | b (-) | sample |
|---|---|---|---|---|
| Leaf+stem biomass | 0.99 (0.73) | -832 | 0.99 (0.99) | 16 (12) |
| Stem biomass | 0.99 (0.83) | -227 | 0.93 (0.88) | 19 (15) |
| Leaf biomass | 0.85 (0.16) | -221 | 0.90 (0.24) | 16 (13) |
| Leaf area | 0.82 (0.56) | -0.4* | 0.82 (0.64) | 19 (16) |
| Standing stem biomass | 0.99 (0.85) | -203 | 0.94 (0.97) | 19 (16) |
| Soil mineral nitrogen | 0.27 (0.10) | 152 | 0.31 (0.29) | 6 ( 5) |

* in units of $m^2\ m^{-2}$

# 9 LIST OF SYMBOLS

| Symbol | Description | Unit | Equation |
|---|---|---|---|
| $\alpha$ | Coefficient relating $u_o$ and decomposition of humus to $T_s$ | $°C^{-1}$ | 422,423,427 |
| $\beta$ | Coefficient relating $u_o$ to litter age | - | 423 |
| $\delta W_{aMax}$ | Maximum daily release of internal stored assimilates | kgDW $ha^{-1}$ $d^{-1}$ | 335,335 |
| $\gamma$ | Light factor used when calculating the canopy photosynthesis | - | 315,316,710, 711,721 |
| $\delta A_i$ | Leaf area index of sublayers in the canopy | - | 721 |
| ' | Denotes the daily change of the symbol concerned | - | |
| (in) | Denotes a positive change of the symbol concerned | - | |
| (out) | Denotes a negative change of the symbol concerned | - | |
| * | Denotes a complete or partly new equation not originating from another publication | - | |
| $A_i$ | Leaf area index accumulated from the canopy top to the bottom of layer number i | - | 712 |
| $a_i$, $b_i$, $c_i$, $d_i$ | Coefficient names used commonly. Index i varies. | differs | 314,424,712 |
| $a_l$ | Fraction of nitrogen in leaves withdrawn to stems before shedding | - | 324,334,413, 420,421 |
| $a_{ld}$ | Fraction of leaf litter lost by leaching | - | 411 |
| $A_{li}$ | Canopy leaf area index | - | 316,324-327, 330,331,710, 713,714,721 |
| $A_{lia}$ | Area of leaf-fall, caused by shedding in autumn, per unit ground area | - | 326,327 |
| $A_{lif}$ | Area of leaf-fall, caused by self shading, per unit ground area | - | 713 |
| $A_{lix}$ | Maximal leaf area index as caused by self shading | - | 713,714 |
| $a_{ln}$ | Fraction of nitrogen in the leached litter substances | - | 413,415,421 |
| $b_A$ | Aerial leaf weight | gDW $m^{-2}$ | 315,324,330, 331,710,715 |
| $b_{Al}$ | Annual fractional increase of the aerial leaf weight. | - | 715 |
| $b_{Ao}$ | Aerial leaf weight of shoots younger than one year | gDW $m^{-2}$ | 715 |
| $b_i$ | Leaf area index to shoot biomass ratio | ha $tonDW^{-1}$ | - |
| $b_{il}$ | Coefficient relating $A_{li}$ to $W_{sh}$ | tonDW $ha^{-1}$ | 330 |
| $b_{io}$ | $b_i$ at unity $W_{sh}$ | ha $tonDW^{-1}$ | 330 |
| $b_r$ | Fraction of daily total growth delivered to roots | - | 320,321,323, 433 |
| $b_{ro}$ | $b_r$ minimum | - | 321 |
| $C_d$ | Amount carbon in the litter | kgC $ha^{-1}$ | 425,426 |
| $c_l$ | Carbon concentration in litter | gC $gDW^{-1}$ | - |
| $c_m$ | Carbon concentration in microbial biomass | gC $gDW^{-1}$ | 425,426 |
| $c_u$ | Fraction of the soil mineral nitrogen possible to be taken up by plant each day | $d^{-1}$ | 430-432,716 |
| $c_{u1}$ | Coefficient for determining $c_u$ as a function of root growth | ha $kgDW^{-1}$ | 716 |
| $c_{u2}$, $c_{u3}$ | Coefficients for determining $c_u$ as function of root biomass | ha $kgDW^{-1}$ $d^{-1}$ | 716 |

| | | | |
|---|---|---|---|
| $c_{uMax}$ | Maximal value of $c_u$ | $d^{-1}$ | 716 |
| D | Daily relative duration of sunshine at unobstructed horizon | h | 314 |
| $d_a$ | Length of the day when leaf abscission starts | h | - |
| $d_l$ | Fraction of leaf biomass at harvest | - | 606,607 |
| $d_Q$ | Fraction of stem biomass older than one year reduced at harvest | - | 606-609 |
| $d_s$ | Fraction of stem biomass younger than one year reduced at harvest | - | 606-609 |
| $e_o$ | Microbial efficiency of carbon utilization | - | 425,426 |
| $g_I$ | Light quanta for overcast conditions as a fraction of clear sky conditions | - | - |
| $g_q$ | Parameter converting global radiation into photosynthesis active light quanta | $\mu E\ J^{-1}$ | 318 |
| $g_s$ | Parameter related to the atmospheric turbidity | - | 318 |
| h | Hour of the day | h | 315,316,318, 710,711 |
| $h_l$ | Fraction of the reduced parts of leaves at harvest that is removed from the plantation | - | 600,603,606, 607 |
| $h_Q$ | Fraction of the reduced parts of stems older than one year that is removed from the plantation | - | 602,605-607 |
| $h_s$ | Fraction of the reduced parts of stems younger than one year that is removed from the plantation | - | 601,604,606, 607 |
| H | Solar elevation | rad | 318 |
| i | Accumulated, from canopy top, number of layers with unity leaf area index | number | 710-712,714, 721 |
| I | Incident light intensity (400-700nm) on a horizontal surface | $\mu E\ m^{-2}\ s^{-1}$ | - |
| $I_d$ | I giving net photosynthesis equal to zero | $\mu E\ m^{-2}\ s^{-1}$ | 714 |
| $I_i$ | I above, an internal canopy layer | $\mu E\ m^{-2}\ s^{-1}$ | 711,714 |
| $I_p$ | Parameter relating photosynthesis to I | $\mu E\ m^{-2}\ s^{-1}$ | 316,711 |
| j | Age of litter or shoot (i.e. two alternatives) | year | 411,422,423, 425,426,715 |
| k | Light extinction coefficient related to leaf area | - | 316,711,712, 714 |
| $k_h$ | Parameter corresponding to the relative decrease in $N_h$ | $d^{-1}$ | 427 |
| $k_{ml}$ | Coefficient related to the rate of leaf-fall | $d^{-1}$ | 329 |
| $k_{mo}$ | Coefficient related to the rate of leaf-fall | - | 329 |
| l | Identification of the single plant | number | 720,721 |
| $l_{Max}$ | Number of plants including in the competition calculations | number | 721 |
| M | Sunshine function relating $P_d$ to $P_{do}$ and $P_{dc}$ | - | 313,314 |
| $m_A$ | Parameter related to the leaf area lost by leaf-fall | - | 327-329 |
| $m_r$ | Parameter related to the death of roots | - | 320,420,421, 433 |
| $m_s$ | Fraction of stems older than one year that die | $d^{-1}$ | 420,421,500, 501 |
| $N_a$ | Total amount of nitrogen available for plant uptake | $kgN\ ha^{-1}$ | 410,411,430-432 |
| $N_{ap}$ | Nitrogen content in the available assimilate pool in the plant | $kgN\ ha^{-1}$ | 410,411,414, 415,609 |

| | | | |
|---|---|---|---|
| $N_{as}$ | Soil mineral nitrogen in the total profile | kgN $ha^{-1}$ | 410,720 |
| $N_d$ | Amount of nitrogen in the litter | kgN $ha^{-1}$ | 411,421,426, 607 |
| $N_f$ | Amount of nitrogen in liquid fertilizers | kgN $ha^{-1}$ | 411 |
| $N_h$ | Amount of nitrogen in | kgN $ha^{-1}$ | 411, 427 |
| $n_l$ | Canopy nitrogen concentration | - | 317,322,415, 421,435 |
| $N_l$ | Amount of nitrogen in the leaf biomass | kgN $ha^{-1}$ | 412,432,435, 603,607 |
| $N_{lfl}$ | Amount of nitrogen leached from falling leaves | kgN $ha^{-1}$ | 411,413 |
| $n_{lMax}$ | Maximum nitrogen concentration in leaves | - | 322,417,432 |
| $n_m$ | Microbial biomass nitrogen concentration | - | 426 |
| $N_{Qr}$ | Amount of nitrogen in roots older than one year | kgN $ha^{-1}$ | 503 |
| $N_{Qs}$ | Amount of nitrogen in stems older than one year | kgN $ha^{-1}$ | 501,605,607 |
| $n_r$ | Root nitrogen concentration | - | 421,433 |
| $N_r$ | Amount of nitrogen in root tissues younger than one year | kgN $ha^{-1}$ | 412,430-433, 503 |
| $n_{rMax}$ | Maximum nitrogen concentration in roots | - | 430 |
| $n_s$ | Stem nitrogen concentration | - | 421 |
| $N_s$ | Amount of nitrogen in stem tissues younger than one year | kgN $ha^{-1}$ | 412,431,432, 434,501,604, 607 |
| $n_{sMax}$ | Maximum nitrogen concentration in stems | - | 417,431 |
| $N_t$ | Amount of nitrogen in all tissues younger than one year | kgN $ha^{-1}$ | 411,412,415-417 |
| P | Canopy carbohydrate fixation rate per unit leaf weight | gDW $gDW^{-1}$ $h^{-1}$ | - |
| $p_1$, $p_2$ | Coefficients relating $P_m$ to $n_l$ | gDW $gDW^{-1}$ $h^{-1}$ | 317 |
| $P_d$ | Daily totals of P per unit ground surface | kgDW $ha^{-1}$ $d^{-1}$ | 311,313 |
| $P_{dc}$ | Totals of P for clear days per unit ground surface | kgDW $ha^{-1}$ $d^{-1}$ | 313,315,710 |
| $P_{do}$ | Totals of P for overcast days, per unit ground surface | kgDW $ha^{-1}$ $d^{-1}$ | 313 |
| $P_m$ | P only limited by leaf nitrogen concentration | gDW $gDW^{-1}$ $h^{-1}$ | 315,317,710 |
| $Q_r$ | Root biomass older than one year | kgDW $ha^{-1}$ | 311,502,608, 609,716 |
| $Q_s$ | Stem biomass older than one year | kgDW $ha^{-1}$ | 311,336,420, 421,500,602, 606,608,609 |
| $r_g$ | Fraction of daily carbohydrate fixation lost by respiration | - | 311 |
| $r_m$ | Fractional respiration losses of $Q_r$ and $Q_s$ at $T_1$°C | $d^{-1}$ | 311 |
| $S_o$ | Solar constant (above atmosphere) | W $m^{-2}$ | 318,319 |
| t | Time as day numbers from 1st of January | day number | 310,319,328, 329 |
| T | Daily mean air temperature | °C | 310,312 |
| $T_1$ | Temperature limit for start of growth | °C | 310,312 |
| $T_2$, $T_3$ | Low and high limit for growth not limited by temperature | °C | 312 |
| $t_a$ | t at start of leaf abscission | day number | 328,329 |
| $T_{Acc}$ | Accumulated temperature sum from day $t_T$ | d °C | 310 |

| | | | |
|---|---|---|---|
| $t_{Dec}$ | Length of decomposition period prior to the simulation start. During these periods a constant air temperature (10°C) and optimum water conditions are assumed | d | - |
| $T_f$ | Function relating growth to T | - | 311,312,335 |
| $t_h$ | t at harvest | day number | - |
| $t_o$ | t at start of the growing season | day number | 310,417 |
| $T_s$ | Daily mean soil temperature | °C | 422,427 |
| $T_{Sum}$ | Air temperature sum since $t_T$ for which growth starts | d °C | 310 |
| $t_T$ | Day number for which the calculation of $T_{Acc}$ shall start | day number | 310 |
| u | Growth rate of microbial biomass per unit carbon | gDW $gC^{-1}$ $d^{-1}$ | 422 |
| $u_o(j)$ | u at 10°C of litter of age j | $d^{-1}$ | 422,423,425, 426 |
| $v_d$ | Water reduction factor for decomposition | - | 422,424 |
| $v_p$ | Water reduction factor for plant growth | - | 315,322,710 |
| $v_s$ | Soil relative water content (by volume) | - | 424 |
| $W_a$ | Amount of assimilates available for flushing | kgDW $ha^{-1}$ | 311,333-336, 416,608 |
| $w_{ai}$ | The fraction of the growth of stem and root that is allocated to the easily available pool. | - | 320,323,334, 415 |
| $w_{as}$ | Parameter equal to the total stem biomass for which $\delta W_{aMax}$ is doubled | kgDW $ha^{-1}$ | 336 |
| $W_d$ | Litter dry weight | kgDW $ha^{-1}$ | 420,606 |
| $W_l$ | Leaf biomass younger than one year | kgDW $ha^{-1}$ | 331,332,417, 432,600,606 |
| $W_{lf}$ | Accumulated leaf-fall during the current year equal to $(1-a_l)b_A A_{li}(out)$ | kgDW $ha^{-1}$ | 323,324,334, 413,415,420, 421,435 |
| $W_r$ | Root biomass younger than one year | kgDW $ha^{-1}$ | 311,320,420, 421,430,502, 608,609,716, 720 |
| $W_s$ | Stem biomass younger than one year | kgDW $ha^{-1}$ | 311,332,336, 417,431,500, 601,606,608, 609 |
| $W_{sh}$ | Accumulated shoot (stem+leaf) growth during the current year. | kgDW $ha^{-1}$ | 323,330,332 |
| $W_t$ | Total biomass younger than one year | kgDW $ha^{-1}$ | 311,320,323, 334,433 |

# 10 ACKNOWLEDGEMENT

Professor Per-Erik Jansson at the Swedish University of Agricultural Sciences (SUAS), Uppsala, made valuable comments of the manuscript. Gunn Persson (SUAS) helped me with the SOIL model simulations. Tom Ericsson, Theo Verwijst and Lars-Owe Nilsson (SUAS) provided unpublished data for the validation. Nigel Rollison made the linguistic corrections. All these persons are greatly acknowledged. This work was done at the Department of Soil Sciences (SUAS) making use of the software especially designed for this type of models and developed by Per-Erik Jansson and Jan Clareus. Much of the basic work concerning the model formulation was done at the Swedish Energy Forestry Project, Department of Ecology and Environmental Research, SUAS, Uppsala and funded by the Swedish Energy Administration.

# 11 SUMMARY

A simulation model for the development of short rotation forests as a function of climate and management is presented in detail and with a direct link to the user's manual aimed for the person running the model. The model simulates, on a daily basis, growth based on the canopy photosynthesis, allocation of assimilates, nitrogen turnover in the soil, and nitrogen uptake based on plant N-demand and N-availability in the soil. The assimilation rate hence determines the nitrogen uptake, which in turn determines the assimilation rate. The stand is assumed to be horizontally homogeneous and divided into compartments of leaves, stems, roots, easily available assimilates, litter cohorts and humus. Driving variables are daily values on global radiation, air temperature, soil temperature, plant water reduction factor, soil water content and N-fertilization rate. As a simulation example, the model is tested for a *Salix viminalis* stand in central Sweden for measurements on leaf biomass, stem biomass, leaf area, leaf-fall and soil mineral nitrogen. The measurements were, with some exceptions, performed about every second week from 1985 to 1988. During this period the stand developed from a recently planted stand to a well-established stand. It was harvested during the spring of 1987 and severely attacked by fungi during the summer of 1987. All these events are considered in the simulation. The model explained 99% of the variations in stem biomass and 85% of the variations in leaf biomass.

*SAMMANFATTNING*

*Här beskrivs en simuleringsmodell för "mini-rotation-skogars" utveckling vid variationer i klimat och skötselmetoder. Beskrivningen är avsedd att kunna användas vid körning av modellen. Modellen simulerar dagliga värden på tillväxt, markens kväveomsättning samt växtens kväveupptag. Fotosyntesens kolupptag påverkar kväveupptaget som i sin tur påverkar kolupptaget. Beståndets som antas vara horisontellt homogent är uppdelat i blad, stam, rot, lättillgängligt assimilat, förna och humus. Drivvariabler är dagliga värden på relativa solskenstid, lufttemperatur, växtens vattenreduktionsfaktor, markvatteninnehåll samt kvävegödsling. Modellen testas mot mätningar på ett Salix viminalis bestånd i Uppsala. Under en fyraårsperiod mättes bladbiomassa, stambiomassa, bladyta, bladens förnafall samt markens mineralkväveinnehåll. Under perioden utvecklades beståndet från ett nyligen planterat bestånd till ett etablerat bestånd, utsattes för svampsjukdomar samt skördades. Alla dessa händelser beaktas vid simuleringen. Modellen förklarade 99% av variationerna i stambiomassa och 85% av variationerna i bladbiomassa.*

# 12 REFERENCES

Papers and reports published with relevance for the WIGO model and publications referred to in the text.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